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CONTENTS

THE PROGRESS OF PLANT SUCCESSION ON THE SOUFRIERE OF ST VINCENT

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(*With Plates* 1 *and* 2 *and* 1 *Figure in the Text*)

INTRODUCTION

The island of St Vincent

The Soufriere of St Vincent is one of the two still intermittently active volcanoes in the West Indies, the other being Mont Pelée in Martinique. The island of St Vincent is one of the most southerly of the Lesser Antilles, lying about latitude 13° N. and longitude 61° W., and forming a part of the British colony of the Windward Islands. The island is roughly elliptical in plan (Fig. 1) with a greatest length of about 29 km. (18 miles) and a greatest breadth of nearly 18 km. (11 miles). Structurally it is a young volcanic pile and is exceedingly mountainous. The dominant feature is a Main Ridge which rises sharply from the sea in the south to Mount St Andrew (742 m., 2433 ft.) and runs slightly east of north through the Grand Bonhomme (974 m., 3193 ft.) to the Morne Garu Mountains and Richmond Peak (1076 m., 3528 ft.). Here there is a deep trough across the island, north of which rises the Soufriere as a solitary cone, its highest point touching 1246 m. (4084 ft.).

St Vincent is well watered, the total annual precipitation rarely falling below 200 cm. at any point. In the mountains the rainfall is probably at least 380 cm. (150 in.) without any effective dry season. The cultivated coastal belt receives 200–255 cm. (80–100 in.), with a dry season from February to May when the ground may become somewhat parched. Hurricanes are of frequent occurrence. The earliest on record occurred in 1780 and did great damage. There was a slighter storm in 1819, severe ones in 1830 and 1886, a slight one in 1897 and a severe blow in 1898. Finally, a moderate hurricane struck the island in 1921.

St Vincent's population is mainly of African descent and averages about 400 to the square mile (155 per sq. km.). Only the lower coastal lands, about two-fifths of the area, are populated. The chief crops are arrowroot, cotton and canes. The interior mountains, aggregating three-fifths of the island's area, are either volcanically devastated or are too steep and inaccessible for even the West Indian peasant to cultivate. A considerable extent of interesting natural vegetation is therefore still in existence.

History of vulcanism

On the discovery of St Vincent by Europeans, aboriginal Caribs were found to live in dread of a potent deity who dwelt at the summit of the great mountain in the north of the island. Propitiatory offerings were made to avert periodic wrathful emissions of fire and brimstone. It is on record that the mountain erupted in 1718, but the island had not then been settled. A second eruption took place in 1812, with some destruction of life and property and a third outbreak in 1902–3 when two thousand persons lost

ST VINCENT

0   1   2   3   4   5

miles

Heights in feet

N

4084

Lake Soufriere

Owia

Overland

Chateaubelair

Richmond Peak
3528

Morne Garu Mountains

Georgetown

Wallilabou

Colonarie

Grand Bonhomme
3193

Petit Bonhomme

Mount
St Andrew
2433

Kingstown

Calliaque
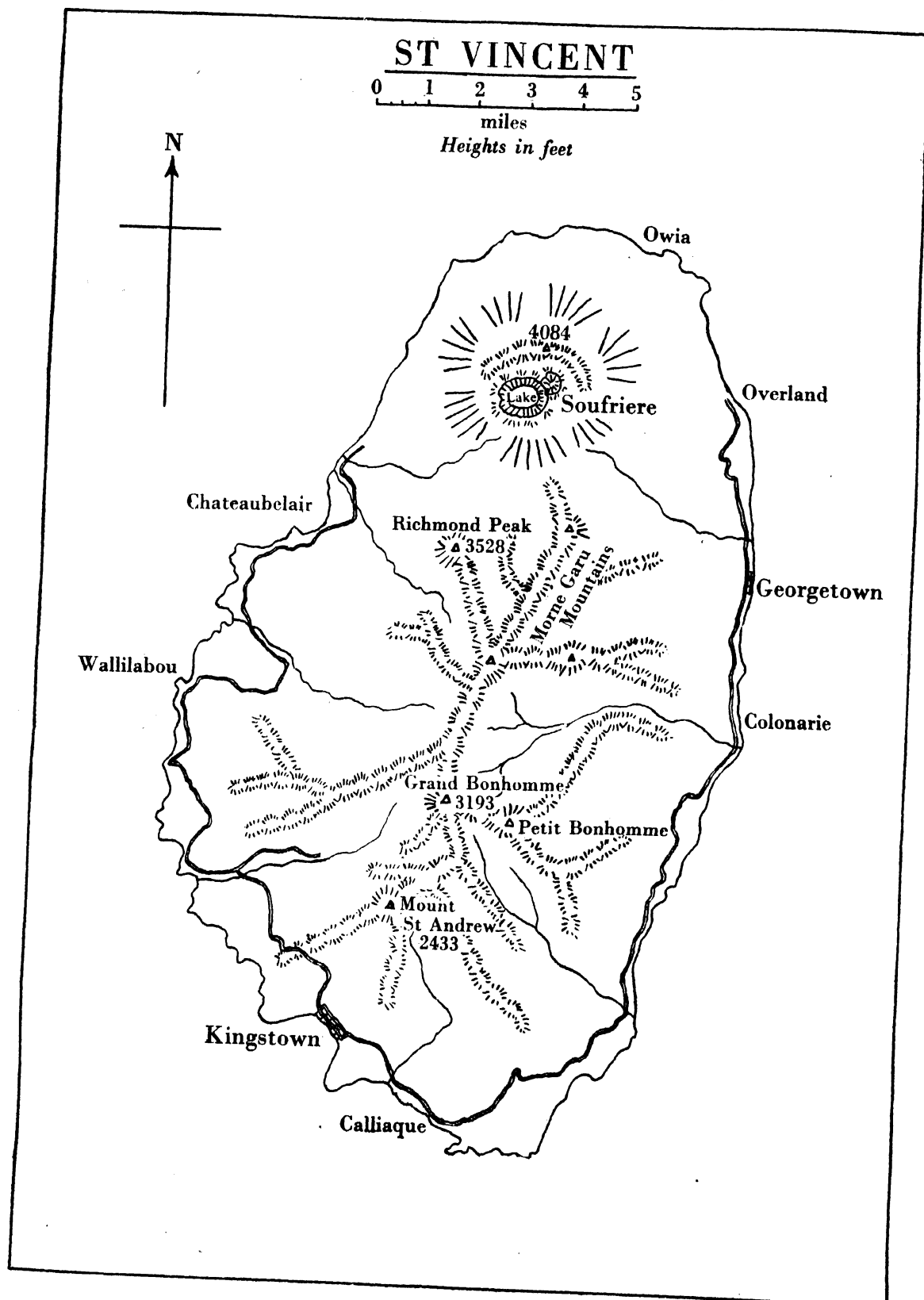
Fig. 1.

their lives. On the last two occasions a rain of dust occurred in Barbados, 100 miles to the east.

Vulcanism in the southern part of St Vincent is long since extinct, but the country is still topographically immature and the soils and rocks are nowhere deeply weathered. The Soufriere being still intermittently active, its slopes are covered with loose debris which is rapidly eroded. The streams descending from it flow only after rain-storms. They rise in active gully systems and, after falling down deep channels, empty into the sea over huge outwash fans of black sand and shingle. The present crater of the Soufriere is about 1·6 km. (1 mile) in diameter and 305 m. deep to the surface of the lake it contains. This lake is of unknown depth and has no outlet. The water is deep green in colour and the inner walls of the crater fall almost sheer to it. The height of the crater rim above sea-level varies around 1000 m., and on the north side, set back about a quarter of a mile (0·5 km.), it is bordered by a remnant of an older, larger crater rim which attains the mountain's full height of 1246 m. (4084 ft.) and which evidently bears the same relation to the present crater as the famous Monte Somma does to the present crater of Vesuvius.

The geology of St Vincent has been described by Earle (1928) and studies of the most recent eruption have been published by Anderson & Flett (1902), Smith (1902), an anonymous writer (1903), Anderson (1908) and Tempany (1917), among numerous others.

The principal events of the eruption of 1902-3 took place as follows. Early in 1902, premonitory earthquake shocks were felt. On 6 May the crater lake boiled and flowed over, clouds of steam were emitted and great detonations heard. Next day, at 2 p.m., a tremendous incandescent avalanche of red-hot dust and steam swept over all the slopes of the mountain and all vegetation appears to have been burned off. Explosive ejections of dust, ashes and lapillae continued at intervals for 12 months, after which the volcano became again quiescent and the crater was sealed. Material was deposited on the mountain slopes to a depth of roughly 1 ft., burying the carbonized remains of the original vegetation.

THE VEGETATION TYPES OF ST VINCENT

The greater part of the forest in the mountains of the southern part of St Vincent, even though it has not suffered from recent volcanic activity, is of subclimax type owing to the regular hurricanes which periodically destroy large trees and thus prevent development of the climax montane rain forest. Ascending towards the Main Ridge, permanent cultivation is mainly found to cease at between 300 and 400 m., the higher land in this island being too steep for settled agriculture, although there is a zone of shifting cultivation where peasants have rented parcels from the Crown and cleared forest to plant vegetables. These 'gardens' are generally surrounded by high rain forest in a good condition as there is little felling of timber, and it has been the practice in recent years to restrict the peasants to felling only old second growth for their gardens. This forest is climax and belongs to the formation lower montane rain forest as defined by Beard (1944). Floristically it belongs to the *Dacryodes-Sloanea* association which is found on all the mountainous islands of the Lesser Antilles.

Lower montane rain forest

The community may be briefly characterized as follows. There is a closed canopy some 25 m. (80 ft.) above the ground, dominant trees attaining about 30 m. (100 ft.). There is a lower tree stratum, a shrub layer and a ground layer. Tree boles are long and clean,

giving the usual columnar effect of rain forest. There are few lianes and crown epiphytes but much moss on trunks and branches. Tree ferns are occasional in the shrub layer which is only moderately dense and composed of young trees and bushes, the latter mainly rubiaceous. A palm, *Euterpe hagleyi*, forms about 25% of the whole forest crop and forms part of the canopy. All the trees are evergreen. Ground vegetation is exceedingly luxuriant and forms a dense knee-high tangle of ferns, moss, Heliconias, small dicotyledonous herbs and tree seedlings. Gommier (*Dacryodes excelsa* Vahl.) is the most abundant tree and forms about 25% of the forest. The Euterpe forms another 25%. Other component trees are sarinette (*Ormosia monosperma* (Sw.) Urb.), ironwood (*Sloanea sinemariensis* Aubl.), wild star apple (*Micropholis* sp.), bullet (*Manilkara riedleana* Pierre), sweetwood (*Lauraceae* spp.), marouba (*Simaruba amara* Aubl.) and horseflesh mahogany (*Hieronyma caribaea* Urb.).

Hurricane forest (Pl. 1, phot. 1)

At about 500 m. (1600 ft.) elevation, as one ascends, the forest suddenly becomes patchy. Big old trees of *Sloanea sinemariensis* are found standing isolated in younger growth of *Inga ingoides*, *Cecropia peltata* and tree ferns (*Cyathea* sp.), or there are young thickets of *Dacryodes excelsa* and its associates mixed with much *Prestoea montana* and *Inga ingoides*. Quite quickly regular subclimax hurricane forest is entered though isolated big trees persist for a while. In some of the more sheltered parts of the mountains such as on Mount St Andrew, secondary timber forest of *Chimarrhis cymosa*, *Manilkara riedleana* and *Daphnopsis caribaea* is found, but as a general rule 'hurricane forest' occupies the whole mountain zone between the lower montane rain forest and the elfin woodland of the highest peaks. Evidently the full force of the wind during the hurricanes which are so frequent in St Vincent is felt above 500 m. elevation. Lower down the forest resists serious damage, but above that level any large trees are periodically overturned, so that development towards the climax is continually being set back. Doubtless the effect of the wind is aggravated by the exceedingly steep slopes and shallow soil which make it difficult for a large tree to obtain a secure root hold. Trees are blown over rather than broken.

In hurricane forest there is only one stratum of trees, which usually form a light canopy about 12 m. above ground though this height is very variable. On steep slopes the trees and palms tend to be drawn up and may exceed 20 m. (70 ft.) in height, whereas on ridges growth is commonly relatively stunted. There is no shrub layer, but the ground layer is tremendously luxuriant and forms a dense waist-high tangle of dank herbaceous vegetation. Ferns, in many species, are the dominant plants in this layer. Occasional patches of tree ferns (*Cyathea*) are found, but commonly the ferns are not of arborescent species. With them are found *Heliconia bihai*, an *Anthurium*, a *Lycopodium*, a *Carludovica* which is usually terrestrial but sometimes also a climber, *Begonia* spp. and other flowering herbs, while the soil is covered with a thick continuous mat of filmy ferns. The trailing silver fern (*Gleichenia*) may be locally abundant. Tree trunks and branches are thickly covered with moss and small climbers.

The palm *Prestoea montana* Nichols is dominant and characteristic. It tends to occur in patches rather than evenly, but on the average forms about 75% of the crop. The hurricane forest therefore could be described as a 'palm brake', but since it is possible that elsewhere true palm brake may occur as a climax formation, it was thought preferable
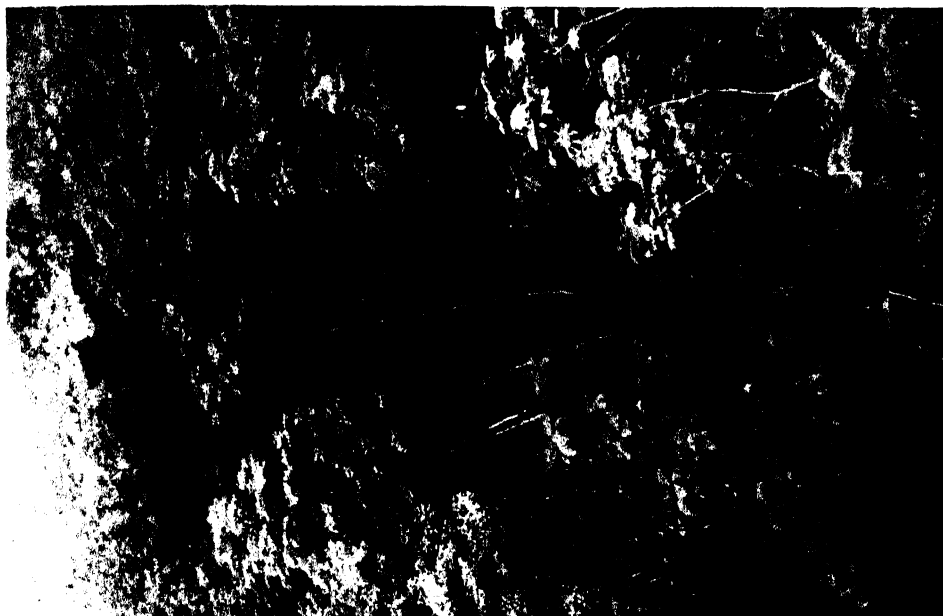
Phot. 2. Tall secondary forest at the base of the Soufriere with *Freziera* and *Cecropia*.

Phot. 1. Hurricane forest on the Morne Garu mountains. Note prevalence of *Prestoea* and the rich herbaceous ground layer. The trees are *Richeria grandis*.

Phot. 3. *Charianthus, Cyathea, Gleichenia* and *Lobelia stricta* at 650 m.

Phot. 4. General view of the crater of the Soufriere.

to adopt a different title for this type in the Antilles which is definitely seral. The trees associated with the *Prestoea* are of few species and small size. Except for an occasional old standard which is evidently a relic of former climax forest, girths do not exceed 1 m. Trunks are very crooked and fork or branch low down. The commonest tree is *Freziera hirsuta* Sm. Other species noted include *Inga ingoides* Willd., *Cecropia peltata* L., *Ficus* and *Clusia* spp., *Richeria grandis* Vahl., and occasionally the palm *Euterpe hagleyi*. At lower levels a few trees of the rain forest are found such as *Micropholis* and *Myrtaceae* spp., *Dacryodes* and *Sloanea*. Higher up typical species of the elfin woodland come in such as *Didymopanax attenuatum* Dene. & Planch. Occasional rubiaceous shrubs are found.

Elfin woodland

Towards the summits of the peaks and the main ridge, an elfin woodland gradually takes shape. At such an altitude the climax formation exhibits naturally a low, gnarled and windswept structure, lower and more reduced than the hurricane forest. For this reason the hurricane winds are no longer an effective factor, and on the highest peaks climax vegetation is once more found. At about 670 m. (2200 ft.) *Didymopanax attenuatum* appears. Here the height of the trees is reduced to 7–10 m. Other characteristic elfin species gradually come in and *Prestoea montana*, *Freziera hirsuta* and *Inga ingoides* drop out.

The elfin woodland belongs to the *Didymopanax-Charianthus* association of many of the Lesser Antilles. There is seldom a closed tree canopy. Trees attain usually from 4 to 10 m. in height, though in very exposed situations the height may be reduced to below 2 m. There is seldom any definite trunk, the tree forking or dividing low down into a system of long, rambling and gnarled branches which tend to point away from the wind. A conspicuous feature is the moss covering, mosses forming a close mat all over the trunks and ground surface and trailing from the branches. Epiphylls are abundant on leaves and all kinds of epiphytes abound—bromeliads, orchids, ferns, a climbing Anthurium. Ground vegetation consists of moss, begonias, filmy ferns, ferns, club moss and razor grass (*Scleria*). The principal species are *Didymopanax attenuatum* (Sw.) March. and *Charianthus coccineus* (Rich.) D.Don. Associated are *Ilex sideroxyloides* (Sw.) Gr., *Ficus* spp., *Richeria grandis* Vahl., *Endlicheria sericea* Nees and *Rondeletia parviflora* Poir., among others.

PLANT SUCCESSION ON THE SOUFRIERE

Before the 1902 *eruption*

In 1886, E. M. D. Hooper, an officer of the Indian Forest Service, published a *Report on the Forests of St Vincent*, which contains (p. 7) the following account of the vegetation of the Soufriere at that time:

There remains to refer to the flora of the Main Ridge summit. This is met with above Cavaleries, on St Andrew's mountain, and is continued for the last 500 ft. to the top. The same plants are to be found at a similar elevation on the slopes of the Soufriere and comprise comparatively few species—none of them attaining any important or useful dimensions. It will be sufficient to quote the *Weinmannia*, the Mountain Cabbage, *Sauvagesia*, *Desmodium*, *Charianthus*, *Lisianthus*, and a dense damp fern growth. A gregarious slender stemmed tree known as the Burnlime is found on the Soufriere below the influence of the sulphurous atmosphere, but already on a soil formed by the eruptions of the crater, higher up the vegetation is reduced to a series of wooded dead stems up to 1 ft. in girth, killed some few years ago by the exhalations from the mountain, and everywhere a carpet of the *Weinmannia*, an *Iris* and a few aroid growths.

The quotation of 'mountain cabbage', which is presumably *Prestoea montana*, indicates the main type as hurricane forest, which is what we should expect assuming that there had been almost complete recovery from the eruption of 1812. The 'burnlime' appears to be *Sapium caribaeum* Urb., which often forms such secondary stands.

Progress up to 1912

In 1902, all was burned off by incandescent avalanches and the remains buried by a layer of volcanic ash. Carbonized remnants of the forest may be extracted to this day from the cinders. At 730 m. (2400 ft.) the writer found a large log, turned to charcoal, buried beneath a foot of ashes.

As soon as the volcano quietened and cooled, plant colonization began. In 1912 W. N. Sands ascended the mountain and published an account of the plant communities which he found (Sands, 1912). Up to 600 ft. Sands found a community of vines and herbs with a few bushes, which he listed as follows:

Gynerium saccharoides H.B.K. (roseau grass).	Stachytarpheta jamaicensis Vahl. (verbena).
Heliconia bihai Sw. and Heliconia spp.	Arundinella martinicensis Trin. (hurricane grass).
Ischaemum latifolium Kunth. (bamboo grass).	*Gymnogramme calomelanos Kaulf. (silver fern).
Ipomoea spp., Vitis sicyoides.	Bushes of the Rubiaceae and Melastomaceae.

Between 180 and 300 m. (600–1000 ft.) the above community was joined by larger masses of *Cyathea arborea* (L.) J.Sm., *Trema lamarckiana* Bl. and two Psychotrias. At 420 m. (1400 ft.), plants were scantily distributed and growth poor. Principal species were *Gynerium* and *Ischaemum*, *Gymnogramme* (*Gleichenia*) and *Cyathea* with *Freziera hirsuta* Sm., *Eupatorium* spp. and a *Lycopodium*. At about 610 m. (2000 ft.) only the mosses and silver fern survived, and above that height only mosses, algae and lichens.

Progress up to 1942

Considerable changes have taken place in the ensuing thirty years. It will be observed from Sands's account that the most luxuriant regrowth was taking place at the foot of the mountain where conditions are at their most favourable and that no higher plants had appeared near the summit. This phenomenon is still observable as one passes through a succession of types from high forest at the foot to a moss and lichen community at the summit. Cultivations of canes, coconuts and peasants' vegetables have now been re-established up to about 370 m. (1200 ft.) elevation on the mountain, up to the point, in fact, where it begins to slope steeply. Immediately above the cultivated area one enters a tall secondary forest 15–27 m. (50–90 ft.) in height (tall on slopes, lower on ridges). This is pictured in Pl. 1, phot. 2. The trees do not exceed 30 cm. (12 in.) in diameter and appear thin, crowded and drawn up. The canopy is a thin one, most of the trees having light foliage. Few species are represented; the following were noted:

Freziera hirsuta Sm. (gunstock)	v.a.	Ficus spp. (fig)	o.
Inga ingoides Willd. (spanish apple)	a.	Ochroma pyramidale (Cav.) Urb. (bois flot)	r.
Cecropia peltata L. (trumpet)	o.	Daphnopsis caribaea Gr. (mahoe)	r.

It will be noted that these are the trees which associate with *Prestoea montana* in the hurricane forest, though the latter species is absent here, perhaps because of insufficient altitude. The forest has an understorey, continuous in places and up to 6 m. (20 ft.) high, formed largely by the tree fern *Cyathea arborea* (L.) J.Sm. with many Melastomaceae,

* Now referred to *Gleichenia*.

Piperaceae, *Psychotria* spp. and *Acnistus arborescens* (L.) Schlecht. The herbaceous ground layer is exceedingly luxuriant and dense, very much as in hurricane forest. Ferns predominate, *Heliconia bihai* is abundant, there are *Begonia* spp., *Lycopodium*, *Anthurium*, *Carludovica* and filmy ferns. The lower parts of tree trunks are very mossy and bromeliads are plentiful.

At 570 m. (1850 ft.) elevation, this forest is only 10 m. high and has become irregular, whole patches being covered with *Cyathea* or the silver fern, *Gleichenia*. A very few *Prestoea montana* appear here and in the silver fern patches one finds the shrub *Charianthus coccineus* (Rich.) D.Don., a *Lycopodium*, a *Pitcairnia* and two grasses.

At 610 m. (2000 ft.) the forest has shrunk to 3 4 m. high, and is windswept, gnarled and simulating elfin woodland. *Charianthus coccineus* forms about 50% of the crop, with *Freziera*, *Inga* and other melastomes. The tree line is passed about 670 m. (2200 ft.). Here silver fern is dominant, with scattered *Charianthus* and *Cyathea* up to 2–2·5 m. high (Pl. 2, phot. 3). *Lobelia stricta* Sw. appears.

At 730 m. (2400 ft.) plants are knee high only, still composed of silver fern with now very stunted *Charianthus* and *Cyathea*, *Pitcairnia*, *Lobelia*, ferns and grasses. *Freziera* and *Inga* are quite absent.

At 820 m. (c. 2700 ft.) *Charianthus* and silver fern begin to thin out, and *Cyathea* is only 60 cm. (2 ft.) high. Towards 900 m. (3000 ft.) the vegetation is simulating 'paramo' and is distinctly alpine in appearance. The ground is entirely and thickly covered with lichens, thallose, foliose and crustose. Higher plants are scattered and tufted and include the *Lobelia* and *Pitcairnia*, several grasses, a *Lycopodium* and a few ferns. *Cyathea* is now at most 30 cm. (12 in.) high, and the general vegetal covering is ankle deep only. The general colour of the vegetation is blue-grey rather than green.

At the highest levels (Pl. 2, phot. 4) one finds a tundra only. The stony ground is thickly covered with lichens and, in between, a few small clumps of *Lobelia* and *Pitcairnia*. The lichens vary greatly in colour, being predominantly grey or orange, and having a striking appearance at a little distance.

The inside of the crater, in spite of the precipitous nature of the cliffs, is covered with plants right down to the water. The principal are a small composite shrub (*Baccharis cotinifolia* Urb.), *Gleichenia*, *Lycopodium*, ferns, grasses and a few *Cyathea*.

Discussion

It is most interesting to note that certain communities found at the upper levels simulate in physiognomy climax formations such as elfin woodland, paramo (alpine meadow) and tundra (Beard, 1944), though the floristic composition in any example is not that of the climax, and the simulated formation is made to appear far below its proper altitude. This simulation is not coincidental. It demonstrates the relationship which formations of the same habitat-group or formation-series bear to one another. In this case the climax communities of the area belong all to the montane series. When the mesophytic communities of any series of habitats are interfered with or destroyed the moisture relations of the environment are temporarily made more adverse. The presence of a vegetative cover itself has an ameliorating effect on conditions, lost when the cover is removed. If, in addition, the original soil is buried beneath a layer of volcanic ashes, the environment deteriorates still further. It is natural, therefore, that the earlier stages of succession will tend to resemble climax types of greater adversity within the

same group or series. If elfin woodland is totally destroyed by a volcanic eruption which deposits a layer of ashes, the first community colonizing the new ground is one resembling the most extreme montane climax, i.e. tundra, owing to the fact that moisture relations have greatly deteriorated but still remain essentially montane. The tundra-like stage is gradually replaced by one resembling paramo, and finally the climax elfin woodland reappears. This succession is taking place on the Soufriere to-day and can be amply proven by reference to Sands's account. Elfin woodland stands to-day, while Sands found only moss and lichen thirty years before.

This generalization of succession applies only to the communities of adverse environment. Communities developing closer to the optimum pass through rather different stages. In their case, since they are close to the optimum, moisture conditions are subject to less deterioration through interference, and the dominating factors in succession become not moisture relations but seed dispersal and light relations. Where interference has led to serious soil deterioration, a herbaceous or low bush stage will be necessary to build up fertility to the point where high forest can return. In general, high forest grows back directly by stages which are proper to it, do not resemble any climax types, and are determined first by seed dispersal and secondly by light relations. The principal components of evergreen tropical forests seem often in their youth to be silviculturally shade-demanders. Not only do they tolerate shade, they may even require it for successful establishment and growth. Forestry has not as yet produced any experimental evidence on this score, but there is some very suggestive recent work on cacao (Cobley, 1942), which in its native surroundings is an understorey tree in rain forest. Such a shade-demander would be unable to compete successfully in the open. The first tree species to arrive in succession are a specialized group not belonging properly to the climax association, light-demanding, not tolerating shade. Their seed is light and carried far by the wind (*Ochroma*) or is attractive to and distributed by bats (*Cecropia*) or birds (*Freziera*, *Guazuma*). These species have a thin foliage and cast only a light shade. Beneath them comes in a definite group of components of the climax association having high light requirements. Typically these are species which spring up in any large gaps in the forest. In youth they prefer a thin shade but will tolerate full illumination. These, of which in the Lesser Antillean montane zone the principal are various Lauraceae, *Simaruba amara*, *Hieronyma caribaea*, *Pithecellobium jupunba*, *Sapium caribaeum* and *Chimarrhis cymosa*, growing up beneath the light canopy of the first arrivals, form a heavier canopy under which the real shade-demanders will come in and reintegrate the climax association. The high forest now covering the lower levels of the Soufriere is evidently well advanced in the *Ochroma-Cecropia-Freziera* stage and is ripe for the arrival of members of the climax *Dacryodes-Sloanea* association. Delay is possibly due to the distance of several miles from the nearest seed trees.

SUMMARY

The vegetation of the Soufriere mountain in St Vincent, British West Indies, was destroyed by an incandescent avalanche at the eruption of 1902–3, and the mountain was subsequently covered by a layer of fresh volcanic ash.

Plant colonization of the bare ground began as soon as the mountain cooled and succession is still in progress.

The contemporary vegetation was described by W. N. Sands in 1912. The writer visited the mountain in 1942 and found that plants had established themselves right to the summit and also inside the crater. Growth varies from a high forest at the base of the mountain to a moss and lichen tundra at the top.

REFERENCES

Anderson, T. (1908). *Philos. Trans.* A, **108**, 243.
Anderson, T. & Flett, J. S. (1902). *Proc. Roy. Soc.* **70**, 353–548.
Anon. (1903). *West Ind. Bull.* **4**, 92.
Beard, J. S. (1944). *Ecology*, **25**, 127.
Cobley, L. (1942). *Trop. Agriculture*, **30**, 43.
Earle, K. W. (1928). *Report on the Geology of St Vincent.* Kingstown.
Hooper, E. M. D. (1886). *Report on the Forests of St Vincent.* London: Waterlow.
Sands, W. N. (1912). *West Ind. Bull.* **12**, 22.
Smith, L. (1902). *West Ind. Bull.* **3**, 271.
Tempany, H. A. (1917). *West Ind. Bull.* **16**, 126.

THE VEGETATION OF SOME HILLSIDES IN UGANDA

ILLUSTRATIONS OF HUMAN INFLUENCE IN TROPICAL ECOLOGY. I

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(With Plates 3–5 and eight Figures in the Text)

INTRODUCTION

It was Milne of Amani (1935) who first used the term 'catena' (a swinging chain) to denote the sequence of soils from hilltop to valley floor; and he showed (Milne, 1936) that the same method may be used to describe the different zones of vegetation to be found in undulating country, where the same series of plant formations is repeated on hill after hill. This concept of the catena as a unit is most valuable for, without it, a concise description of vegetation in Uganda and in many other parts of East Africa would be impossible; if the different plant associations were to be plotted, a very large scale map would be needed and the result would be a jumble of strips and blocks of forest, woodland, grassland, cultivation and swamp, very hard to interpret except in relation to the relief of the country.

The term is not only convenient in describing the countryside, but also it is justified by the way in which the catena is a biologic unit; for all zones, from hilltop to valley bottom, have special functions in the life of the people and of the animals.

Each zone of the catena must make its contribution to the economy of native life. Therefore the land is divided up in a manner to allow access to all zones: in Uganda the boundaries between the villages usually lie along the centres of the valleys. In parts of the Gold Coast the boundaries are along the ridges of the hills; and, when land is divided up for cacao cultivation, it is not in compact blocks, but in narrow strips stretching across the valley. A similar distribution of land may be seen in the long narrow farms of Wiltshire, which stretch from the water-meadows by the rivers, past the homesteads, over the more fertile lower slopes, to the thin stony soil on the tops of the downs.

An attempt is made to convey an impression of the vegetation of a portion of Uganda by describing some catenas on hills in different parts of the country (Fig. 1). One of these hills is on the Sese Islands, which lie in the north-west corner of Lake Victoria; the others are in the Mengo district on the mainland lying between Lake Victoria and Lake Kyoga, about 150 km. to the north. The country is made up of a vast peneplain sloping northwards from the basin of Lake Victoria, at an altitude of 1120 m., down to the basin of Lake Kyoga, at an altitude of 1015 m. The peneplain has been much eroded; near Lake Victoria there is a succession of flat-topped hills, rising to heights of nearly 200 m. above the lake, and there are no large areas of level ground; but the configuration of the country becomes progressively flatter to the north, with low hills and broad valleys near Lake Kyoga.

The rainfall decreases from south to north: it is over 2000 mm. on the Sese Islands and less than 1000 mm. near Lake Kyoga; as Lake Kyoga lies only 1° 30′ north of the equator, the whole area lies in the belt of equatorial rains, with two wet seasons and two dry seasons each year. The differences in the rainfall are shown by the diagram of the rainfall of three stations—Kalangala on the Sese Islands, in the south, Bukalasa near the centre, and Nakasongola in the north (Fig. 2). There is a slight increase in mean annual tempera-
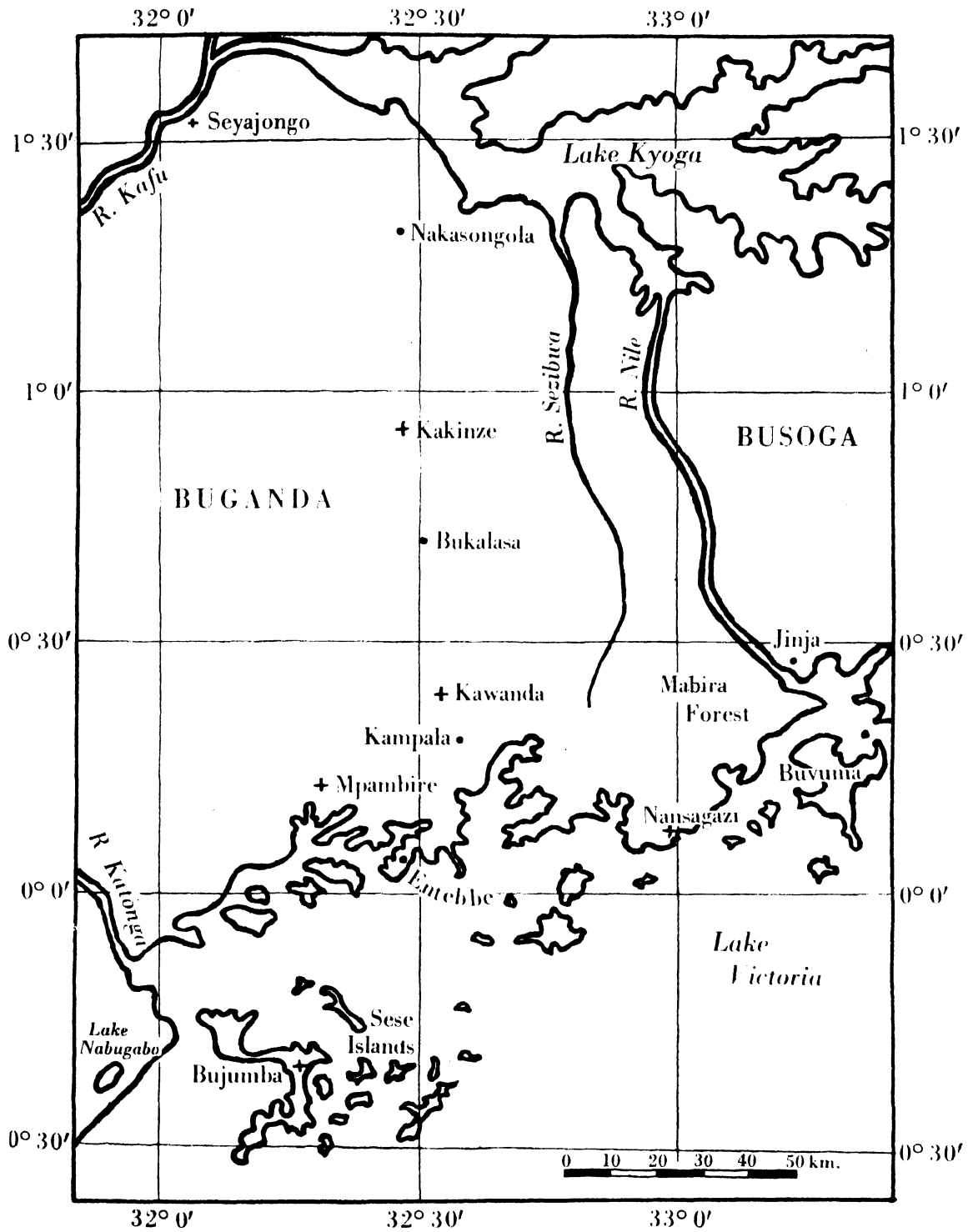
Fig. 1. Map of part of the Uganda Protectorate.
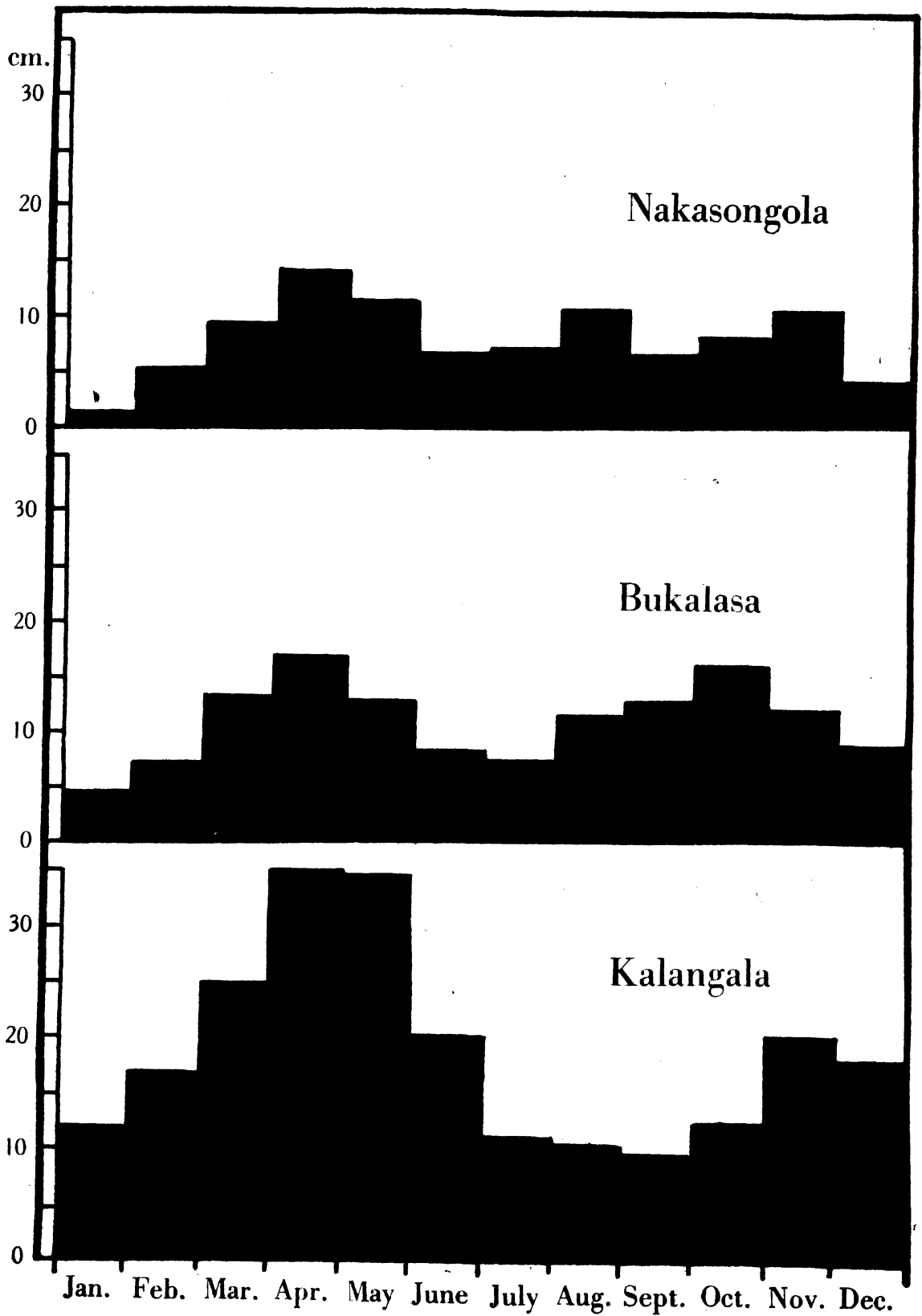
Fig. 2. Average monthly rainfall at Kalangala, Bukalasa and Nakasongola.

ture from south to north; the average on the Sese Islands is under 22° C. and the average near Lake Kyoga is about 1° C. higher. But these averages do not convey the real differences between the temperatures, which are better shown by the mean daily ranges; that on the Sese Islands is less than 8° C., while that near Lake Kyoga is about 13° C. The average humidity decreases from south to north and, during the two dry spells of the year, it falls very low in the region of Lake Kyoga; whereas on the Sese Islands, surrounded by Lake Victoria, it remains fairly high even in the months when little rain falls.

On each of the hillsides described, there are considerable differences between the vegetation of the different zones—the top of a hill may be under woodland or forest, and the sides may be under open grassland. On some of the hillsides, a large proportion of the ground is under cultivation; even in places where there is now little settlement, the effects of human interference with the vegetation are clearly seen. An attempt, therefore has been made to describe the vegetation as it really is, and not to use the method so often employed in tropical ecology—of giving a general description of a region, paying attention to the 'natural' vegetation and neglecting the 'induced' types; for in Uganda it is very difficult to draw a line between the two. The life form and the more important species in each zone are mentioned; and, as the zones are in the belts along the hills, the width of a zone gives an indication of its relative area.

Short descriptions and the results of simple tests are given in respect of the soils encountered. These tests are from small composite samples of the surface soil, taken at a depth of about 10 cm.; the reactions have been tested with B.D.H. Universal Indicator; and the available plant nutrients—phosphates, potassium and calcium—have been estimated by Spurway's approximate methods, the amounts being stated on a scale of 0 to 4, ranging from complete lack to great richness. The nitrates have not been estimated, as it has been found that they show violent fluctuations according to the weather and to the amount of vegetation, and especially of the grass vegetation, on the spot sampled. Even though the results of these examinations are not highly accurate (pH determinations with B.D.H. Universal Indicator do not correspond with those from electrolytic determinations) yet it is felt that they do give a useful guide to the characters of the soils. Furthermore, it is only the surface soils which have been tested, for there has not been the time to dig, to measure and to plot the soil profiles; in many places, however, the subsoils have been exposed in ditches or pits and it has been possible to examine and record their character.

BUJUMBA

The hillside at Bujumba lies on Bugalla, the largest of the Sese Islands, in the north-west of Lake Victoria; Bujumba is situated about 0° 20′ S. and 32° 18′ E. The top of the hill is about 100 metres above the level of the lake and the land slopes steeply to the south-east, down to the channel which separates Bugalla from the next island, Bunyama (Fig. 3).

A general description of the vegetation of the Sese Islands has been published (Thomas, 1941) but, in order that it may be compared with that of the mainland to the north, the vegetation of the hillside at Bujumba is described in some detail. The catena at Bujumba is typical of the Sese Islands, although some of the species there (such as *Lovoa brownii* in the upper forests) are less common in other parts, and other species (such as the fern *Gleichenia linearis*) which are common in other parts of Sese, are not seen at Bujumba.

Nevertheless, the actual zones at Bujumba are representative of the islands; they consist of the following:

A. Hilltop cultivations.
B. Hilltop forest.
C. Tall grass and shrubs at forest edge.
D. Hillside grassland and termite mound complex.
E. Lakeside forest.
F. Aquatic vegetation.

A. *Hilltop cultivations*

The top of Bugalla Island is flat and it is over 1 km. wide at Bujumba; almost all of this land has been cleared from forest and used for cultivation. A few forest trees have been retained, of species which do not compete unduly with crops planted in their
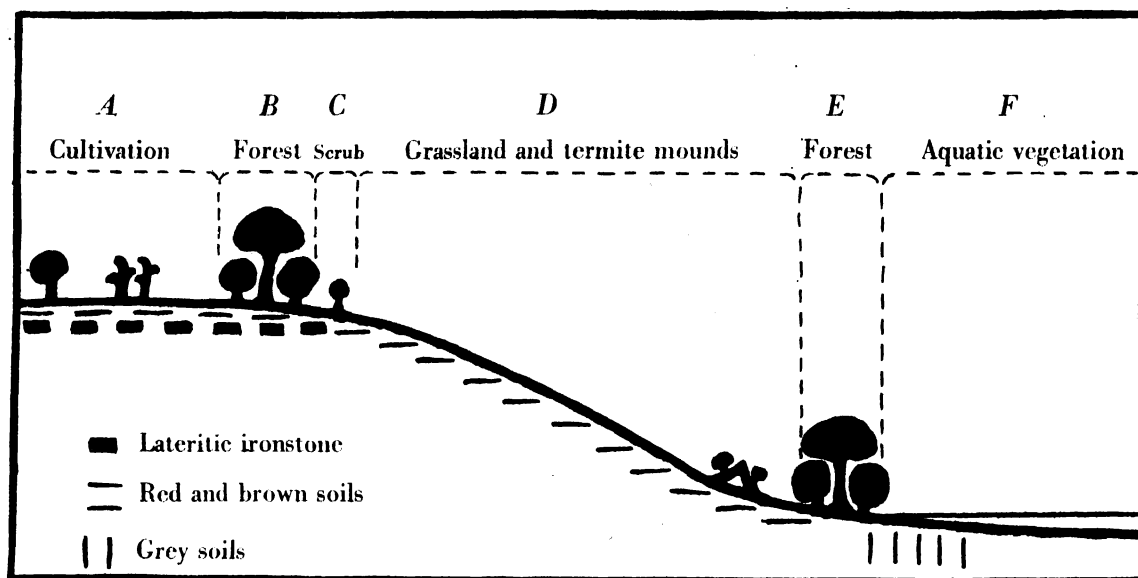
Fig. 3. Diagram of catena at Bujumba.

vicinity, and these stand out among the shorter plants on the farms. The largest specimens are of *Canarium schweinfurthii*, which are only about 20 m. high but have an enormous spread; some of the trees of *Antiaris toxicaria* are nearly as large; the short-lived *Maesopsis eminii* are of more slender growth.

Other trees growing in this zone have been planted. There are many trees of *Ficus natalensis*, whose bark is removed and beaten out to furnish a rough but useful cloth. There are groups of small trees of *Coffea canephora* (Robusta coffee) near the houses; some of these trees are known to be about 100 years old, for there is a long tradition of the cultivation of this crop on the Sese Islands. And there are fruit trees—oranges and mangoes and guavas.

Small patches of bananas are growing near the houses, for it is only in such places that the soil is good enough for them; the bananas are mostly varieties of *Musa sapientum*, whose fruits are used for beer-making, as these types tolerate poor soils better than do the varieties of *Musa paradisiaca*, the plantain, whose fruits are cooked and eaten. In spite of the heavy rainfall and of the fact that only the more hardy types of banana are

planted, yet their growth is stunted in comparison with that to be seen in many drier areas of the mainland of Buganda; this fact is an indication of the poor supply of bases in the Sese soils, for deficiency of potash is often a limiting factor to the growth of bananas.

The sweet potato, *Ipomoea batatas*, and cassava, *Manihot utilissima*, are the main food crops in this area, and there are scattered plots of them; the annual bean, *Phaseolus lunatus*, is grown in admixture with them. None of these three crops—sweet potatoes, cassava and beans—requires a rich soil; but nevertheless a large proportion of the land has been abandoned so that it may recover its fertility; less than one-half of the farmlands at Bujumba are being cropped. Plots which have been left uncultivated soon become colonized with ephemeral grasses such as *Digitaria velutina*, and annual composites such as *Bidens pilosa*, and the succulent spreading *Commelina nudiflora*; and, after a few months, a thicket of coarse herbs such as *Leonotis nepetaefolia* and subshrubs such as *Triumphetta tomentosa* and *Indigofera arrecta* appears. After the land has rested under such vegetation for a few years, it is cleared and dug deeply to remove the rhizomes of *Digitaria scalarum*, a most pernicious couch grass, and more crops are planted; often the whole depth of the soil, which is very friable and lies to a depth of about 50 cm. over a pavement of ironstone, is worked over. This farmland therefore consists of a complex of small patches of bananas, of plots of other food crops, and of fallow land in different stages of recovery; it is noteworthy that elephant grass, which regenerates so rapidly on abandoned farmlands in other wet parts of Uganda, is not common on the Sese Islands—only a few small patches are to be seen at Bujumba in places where the soil is of a fertility above the average.

B. *Hilltop forest*

At the edge of the flat top of the hill, there is a belt of forest which has been retained when the clearings were made for farms. These strips of forest are of great value as windbreaks to protect the farms from the violent storms which sweep over the islands and they are a feature of the Sese landscape, obscuring all signs of cultivation and habitation from the distant view; if it were not for the canoes drawn up on the shore, and for the paths leading up the hillsides, the islands would appear to be uninhabited.

The forest at Bujumba is only about 50 m. wide. It consists of a dense mass of evergreen trees and climbers and is usually about 15 m. high, although in some places there are large gaps where trees have been felled to provide timber for canoe making; not only do the people of Sese need many canoes for their own fishing, but also they make many for sale to fishermen on the mainland.

Maesopsis eminii is the dominant tree; there are few specimens over 20 m. high and the trees are much less vigorous than those to be seen in many forests of the mainland; it is probable that the stunted growth is due both to the high winds and to the poor shallow soil at Bujumba. *Lovoa brownii*, with its dense crown, is also common. Other smaller trees include *Sapium ellipticum*, *Croton sylvaticus*, *Voacanga obtusa*, *Anthocleista schweinfurthii*, *Barteria fistulosa* and the palm *Raphia monbuttorum*.

In places where no large trees have been cut down recently, the overhead canopy is dense and the undergrowth is sparse. *Dracaena fragrans* and *Lasianthus seseensis* are the most common shrubs. There are few herbs, and the soft sandy loam of the forest is incompletely covered with a litter of fallen leaves.

The outside edge of the forest is rich in climbing plants, such as the scandent shrub *Alchornea cordifolia* and the liane *Landolphia florida*; and there is an abundance of the

small soft-wooded tree, *Smithia kotschyi*, growing to a height of about 3 m. on the fringe of the forest.

C. *Tall grass and shrubs at forest edge*

The upper forest extends nearly to the edge of the flat hilltop and, between it and the short grass which covers the hillsides, there is a narrow zone of tall grass and subshrubs: on other hills, where the forest does not cover all the top, this tall grass zone is much more extensive.

At Bujumba, the zone is only about 20 m. wide. On the upper side, it is characterized by the abundance of *Smithia kotschyi* growing in a thicket about 3 m. high. *Pteridium aquilinum* is abundant: the subshrub *Dissotis brazzaei* is common.

These species are mixed with tall tufts of *Hyparrhenia diplandra*, the dominant plant in the zone; it grows as large clumps, about 0·5 m. across, with long erect leaves and inflorescences 2 m. high. There is another grass intermixed with the *Hyparrhenia—Eragrostis blepharoglumis*—which grows in smaller tufts about 1 m. high; this grass is usually most abundant on shallow soils, near outcrops of rock. The soil at the top of the slope is shallow and rocky, being only about 30 cm. deep, with much admixture of lateritic gravel and overlying an outcrop of quartzite with a thin capping of ironstone.

D. *Hillside grassland and termite mound complex*

Almost the whole slope of the hill, for a width of nearly 1 km., is covered with a complex of grassland and numerous termite mounds, which are often associated with groups of woody species. The termite mounds are very numerous near the base of the slope and there are also several near the top, but the middle of the slope is largely an unbroken stretch of fairly short, sparse, grassland.

Loudetia kagerensis is dominant throughout this grassland. It grows in small tufts about 10 cm. wide and raised about 5 cm. above the surface of the ground; there are many small termite runs on the surface of the ground and in the tufts of grass. When the grassland has been burnt over, it may be seen that the tufts cover only half of the surface of the soil—the rest is exposed; yet, even though the slope is steep, there is no perceptible soil wash under this sparse cover of grass. When the grass has been destroyed, as on the paths running down the hill, the soil erodes rapidly, forming gullies up to 3 m. deep. These gullies reveal that the soil has an even red brown colour and a uniform fine texture from near the surface to that depth. In other places there are outcrops of quartzite and the soils near them are much more shallow; yet, in spite of the shallowness of the soil, the dominant grass around the outcrops is *Eragrostis blepharoglumis*, a species which demands a higher grade of soil fertility than does the *Loudetia*.

There is a slight admixture of other species of herbs with the *Loudetia kagerensis* in the grassland—the grasses *Ctenium concinnum* and *Andropogon dummeri*, and the dwarf rounded subshrub, *Indigofera capitata*. The grasses have a slender tufted habit like that of *Loudetia kagerensis*, so that there is never more than a thin cover, about 60 cm. high, over the ground. This grassland is burnt over sometimes during dry spells, but there is little vigour in the fire—some patches remain unburnt and the stems of *Hyparrhenia diplandra* at the top of the slope are only scorched and remain standing.

A quite different type of vegetation is to be seen near the termite mounds. Tufts of *Hyparrhenia diplandra* often grow on the mounds and woody plants grow near the base of them. The usual pioneer species are the subshrub *Dissotis brazzaei* and the shrub

Erlangea tomentosa; then a few seedlings of *Harungana madagascarensis* become established, and grow into small trees. Other trees spring up and there soon appears a large group of woody plants, growing in a ring around the base of the mound and hiding it from view—but the mound will still increase, for the termites will still be active.

A mature colony of woody plants around a termite mound will be about 15 m. across and 10-12 m. high. *Maesopsis eminii* and *Sapium ellipticum* are the most common trees and *Vitex fischeri* is frequent. A ring of *Harungana* usually grows outside the trees, with *Erlangea* and *Dissotis* outside the *Harungana*. Woody climbers—*Landolphia florida*, *Mussaenda arcuata* and *Canthium venosum*—are common. The largest of these colonies are usually close to the upper or lower edges of the grassland and they spread slowly until they become merged into the forests.

E. *Lakeside forest*

The hillside grassland ends abruptly near the bottom of the slope, where the lakeside forest rises up like a wall. This forest, which is about 100 m. wide, is composed mostly of *Uapaca guineensis*, a quick growing tree with prop roots and dense rounded crown of large glossy leaves, which are bronze when young.

On the landward side of the forest *Uapaca* is dominant and, as mentioned above, its thick foliage forms a wall at the edge of the grassland, rising to a height of about 12 m. The canopy of *Uapaca* in the centre of the forest is broken by the crowns of other, taller trees—notably *Maesopsis eminii* and *Piptadenia africana*; *Voacanga obtusa* is also common, but it seldom is taller than the *Uapaca guineensis*.

Memecylon myrianthum, a small tree 3 or 4 m. high, is common in the undergrowth of this forest. *Lasianthus seseensis*, a shrub with small pink flowers and china-blue berries, is dominant in the undergrowth, attaining a height of about 1·5 m. Much of the ground is bare, for the *Uapaca* casts a dense shade; but in some places the small creeping herb, *Geophila hirsuta*, is common.

The forest stretches right down to the edge of the lake, where there is a belt of *Raphia monbuttorum* growing in the moist soil. Intermixed with these palms there is an abundance of the scandent shrub, *Alchornea cordifolia*, which in some places forms a dense thicket. The soil of the lakeside forest is a red loam, brighter in colour and heavier in texture than that of the grassland above. There are many termite mounds in the forest; some are of the small rounded form made by a forest species; others are of the large, conical shape, made by *Termes bellicosus*, such as are to be seen in the grassland above. The large mounds near the upper edge of the forest are still active, but those lower down are old and seem to be deserted; it seems that the forest is extending upwards, both by a slow growth of *Uapaca guineensis* into the grassland and by the spreading and coalescence of the groups of trees growing around termite mounds.

F. *Aquatic vegetation*

In the shallow water, up to a depth of about 1 m., outside the zone of *Raphia* palms, there are growing the rushes *Scirpus corymbosus* and *Eleocharis* sp. And in deeper water, up to a depth of nearly 2 m., there are growing the aquatic grasses *Panicum repens* and *Paspalidium geminatum*; they are rooted in the sandy bottom of the lake and have stems up to 2 m. long, with leaves and inflorescences protruding above the surface of the water.

This zone of vegetation, which is inconspicuous and is only about 50 m. wide, is of considerable importance on account of the fish, especially the small species called 'nkeje', which it contains. Fishing is the main industry of the Sese men; and the sale of fish for consumption on the mainland is their main source of income, for they are skilled in the construction and handling of canoes and can earn money more easily by fishing in the lake than by agriculture on their poor island soils.

Bujumba soils

No.	Zone	Situation	Character	pH	P	K	Ca
1	A	Banana garden	Light brown loam	6·0	3	4	2
2	A	Abandoned farmland	Light brown fine sand	4·5	1	1	1
3	B	Upper forest	Brown sandy loam	5·0	1	2	1
4	C	*Hyparrhenia diplandra* grassland	Brown loam, mixed with lateritic gravel	4·5	1	3	1
5	D	*Loudetia kagerensis* grassland	Light brown fine sand	4·0	1	2	0
6	D	Colony around termite mound	Brown sandy loam	4·5	1	4	1
7	E	Lakeside forest	Red-brown sandy loam	4·5	2	3	0

The richest soil—or rather the least poor soil—sampled at Bujumba is that in a patch of bananas close to a native house, in a place where fertility is maintained by the dumping of household refuse. This soil is only slightly acid in reaction and is fairly well supplied with phosphorus, potassium and calcium. All the other soils are very acid, even that of the abandoned farmland, which lies less than 30 m. away from the banana patch; this land is so poorly supplied in nutrients that its cultivation, even for a crop like sweet potatoes which will grow on a poor soil, is no longer worth while.

The land in the uncleared upper forest, zone B, is only a little less acid and a little better supplied in bases than that of the abandoned farmland; it is much poorer than that of the banana gardens close to the house—land which, by the addition of household refuse, probably is now better supplied with nutrients than it was when under forest. The shallow gravelly soil (sample 4) under coarse *Hyparrhenia diplandra* grass at the edge of the forest is even poorer.

But the poorest soil of the whole catena is that taken in the *Loudetia kagerensis* grassland on the side of the hill (sample 5); this soil is very acid and the test failed to reveal any lime at all in it, a result which has been obtained previously by careful quantitative analysis of similar Sese soils. The poverty of such soil will explain the fact why, in spite of its great depth, it will support only a thin cover of *Loudetia kagerensis*, a grass whose growth both above ground and below ground is so weak that it is displaced by other species on all but the poorest soils. In contrast to the grassland soil, sample 6, taken at the base of an anthill where trees were growing, is better supplied in bases and contained some lime, so it can be understood why the trees can grow there and not in the grassland.

Similarly, the soil of the lakeside forest (sample 7) is better supplied with nutrients, although it contains little or no lime; this sample was not taken near one of the anthills in this forest.

Discussion on Bujumba

The distribution of vegetation on the Sese Islands, especially in its relationship to soil fertility, has been discussed before (Thomas, 1941). Briefly, it has been postulated that it is the supply of nutrients which controls the growth of plants for, under the heavy rainfall and equable temperature of the Sese Islands, it would be expected that evergreen forest would soon cover all the countryside; yet, when the islands were evacuated for

about twelve years on account of sleeping sickness, the forest soon covered the farms but could encroach only slowly on the grassland.

Although the islands have been repopulated for over fifteen years, yet there is little pressure on land. A great deal of the upper forest at Bujumba has been cut down to make farms, but owing to the low fertility of the land, much of it must soon be abandoned to recover under a fallow of shrubs and subshrubs. The trees which have been cut out were mostly fairly small ones, which had grown up after the inhabitants had left the island; the large specimens of *Canarium schweinfurthii* and *Antiaris toxicaria* were retained. These large trees obviously had not grown up under forest conditions, which would have induced a tall bole and a high canopy of branches; their short trunks and huge spread of branches show that they have developed in the open and that the land had been under farms when these trees were young.

It is impossible to discover the age of these trees; they may be anything from 100 to 200 years old: one old coffee tree near Bujumba was known to be nearly 150 years old when it died. But there is no doubt that the Sese Islands have been inhabited for a very long time; stone age artefacts occur there. And tradition avers that, owing to their protection by the waters of the lake, the people on Sese had reached an intensity of settlement long before the people on the mainland—who were liable to continual wars and raids—had done so. One fact is significant; the principal former deities of the Baganda, who appear to represent definite people of past ages, were all derived from the Sese Islands.

It is probable that the Sese Islands at the present day show the effects of long continued and intense human settlement on soils which were not originally rich, for they were derived mostly from acid granitic rocks or from sandstones and quartzites. The deep sandy soils of the hillsides are so poor that they can be used for few crops; in the Bukoba district of Tanganyika, where conditions of soil and climate resemble those of Sese and where there is a great pressure of population, patches of these poor grasslands are sometimes cultivated to grow the Bambara groundnut (*Voandzeia subterranea*) and the tuberous *Coleus dysentericus*, crops which give very poor yields but which are the only ones which can be grown. Before the outbreak of sleeping sickness, about 1900, the Sese Islands were very densely populated and there was great pressure on land; the Sese people used to carry earth and spread it over exposed flat ironstone pavements on tops of the hills, for it was better to go to all that trouble rather than to attempt to grow crops on the deep, but intensively leached, sandy soils of the hillsides.

The normal process of soil leaching by percolating rain water would lead to an accumulation of nutrients at the base of the slope, close to the shores of the lake; this, no doubt, is the reason why there is a belt of slightly richer soil on which the lakeside forest is growing. And the accumulation of nutrients is also carried out by termites, around their mounds (Thomas, 1941 and Thomas, 1944), a fact confirmed by analyses and by the local concentration of woody plants which cannot grow in the poor grassland soils.

But ordinary soil forming processes will not explain why, under so heavy a rainfall, there should be a concentration of plant nutrients in the belt of relatively good soil on the top of the hill. This concentration does not appear to be due to any 'natural' soil forming process, but to long continued settlement. The Sese people have lived on the hill-tops, partly for safety from raiding parties—the peace that the islands enjoyed was only relative, and they were sometimes raided by the inhabitants of Buvuma Island—and also

to avoid mosquitoes which swarm by the lakeshore at night, but which are scarce on the exposed hilltops. Where the people live, there is concentrated the refuse of their food and the ashes of their fires; there the livestock, which have grazed on the hillsides by day, return at night, and their excreta help to enrich the soil still more; kraal manure will produce spectacular effects when it is supplied to bananas growing on the poor Sese soils. Furthermore, the existence of the extensive ironstone pavements, which are more or less horizontal, helps to retain plant nutrients on the hilltops, slowing up the percolation of water through the soil.

NANSAGAZI

The hillside at Nansagazi is situated near 33° 0′ E. and 0° 6′ N., sloping down to the northern shores of Lake Victoria. The prevailing wind is from the south, over the lake, and the rainfall is good and well distributed, amounting to about 1600 mm. per year.
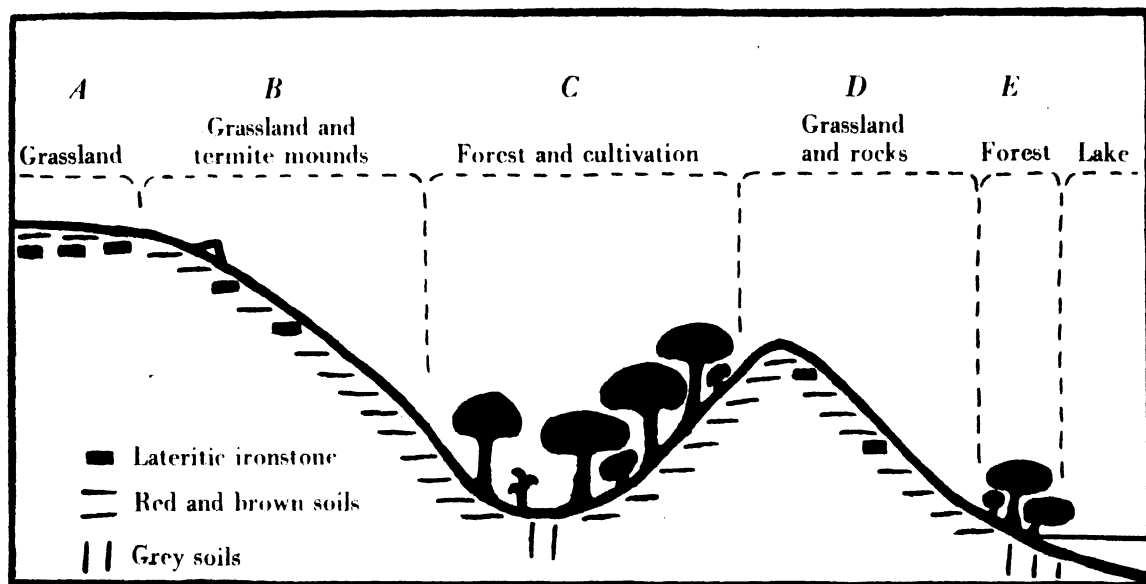
Fig. 4. Diagram of catena at Nansagazi.

As will be seen from Fig. 4 and Pl. 3, phot. 1 the hillside is interrupted by a deep valley parallel to the lake, a feature to be seen in other places along the coast. In consequence of this valley, the catena is a complex one, consisting of five zones:

A. Hilltop grassland.
B. Complex of grassland and termite mounds on upper slopes.
C. Complex of forest and cultivation in the valley.
D. Grassland on rocky slopes above the lake.
E. Lakeside forest.

A. *Hilltop grassland*

The level hilltop is covered with short sparse grassland growing in the thin layer of soil overlying a cap of ironstone: in some places this cap is covered with about 10–15 cm. of soil, in other places it is exposed and, at the edges of the plateau, it forms an outcrop of broken rock and gravel. The bare sheets of ironstone are a very noticeable feature of the grassland: in some places they are nearly level, but there is one especially striking

outcrop of a circular boss, surrounded by concentric rings of ironstone sloping gently outwards.

In places where the soil is only about 5 cm. deep on top of the ironstone, there are scattered tufts of the short grass *Microchloa kunthii*. In places where the soil is deeper, *Loudetia kagerensis* is the dominant species, growing in small tufts and reaching a height of about 70 cm. It is intermixed with other grasses, notably *Eragrostis chalcantha*, *Ctenium concinnum*, *Hyparrhenia filipendula* and *H. dissoluta*. All of these grasses grow in small tufts and are dwarfed in habit, for the pasture is heavily grazed by large herds of cattle and is burnt over once or twice a year; after the grasses have been burnt, it can be seen that they cover only about half the surface of the ground.

There are a few termite mounds on the top of the hill; on and around them taller grasses, which are 1 m. or more high, are growing; the most common species are *Hyparrhenia dissoluta*, *H. diplandra*, *H. filipendula* and *Cymbopogon afronardus*.

B. *Complex of grassland and termite mounds on upper slopes*

The soil on the hillsides is redder than that on the hilltops and, although in some places there are outcrops of quartzite or ironstone, yet the soil is usually deeper than that on the top of the hill. The grass, too, is taller; *Hyparrhenia dissoluta* is the dominant species, reaching the height of 1 m. and, with its glaucous leaves and yellow stems, it produces the general effect of very light colour. The other species with which it is inter-mixed—*Loudetia kagerensis*, *Ctenium concinnum*, *Andropogon dummeri* and *Hyparrhenia filipendula*—are all shorter and obscured when the *H. dissoluta* is fully grown.

Termite mounds are very numerous on the slope; there is a taller growth of grass on them and around them—*H. diplandra* is the common species on the mounds at the top and *Cymbopogon afronardus* is dominant on the mounds near the bottom of the slope. The bracken fern, *Pteridium aquilinum*, grows around some of the lower termite mounds. The lowest mounds, down in the valley, are covered with woody elements, somewhat similar to those of the termite mound colonies on the Sese Islands—*Harungana madagascarensis* is a pioneer species; *Polyscias fulva*, *Pycnanthus kombo* and *Sapium ellipticum* are common trees and *Landolphia florida* is a common climber. As on the Sese Islands, so also at Nansagazi, there appears to be a concentration of nutrients at the bottom of the slope, for *Cymbopogon afronardus*, a species which is confined to termite mounds on the hillside, becomes the dominant species over the lower fringe of the grass-land.

C. *Complex of forest and cultivation in the valley*

At the beginning of the twentieth century, before the outbreak of sleeping sickness necessitated the removal of all the inhabitants on the islands and the northern shores of the Lake Victoria, there was a population of 400 people in the narrow valley at Nansagazi; their farms stretched up the southern slopes of the valley and, to a lesser extent, up the northern slopes as well. When the farms were left, they were soon overgrown, and now most of the valley is covered with forest. This forest is of evergreen trees, and has an uneven canopy; large spreading crowns of old trees of *Chlorophora excelsa* and *Canarium schweinfurthii* stand out from a mass of smaller, more soft-wooded trees; the large old trees had developed when the valley was covered with farms, the smaller ones have developed more recently.

Maesopsis eminii, *Polyscias fulva* and *Pycnanthus kombo* are the most common of the younger trees on the sides of the valley and form a canopy about 10–15 m. above ground, intermingled with a mass of woody climbers—*Landolphia florida*, *Clitandra orientalis* and a number of other species. The coffee-like *Tarenna pavettoides* is abundant as an understorey tree; a few relict *Coffea canephora* and even a few clumps of bananas have persisted, although it is over 35 years since the farms in which they were growing were abandoned. In places where the shade is dense the forest grass, *Leptaspis cochleata*, is dominant near ground level; in more open places, *Renealmia* sp. is abundant. On the steep ground at the west end of the valley, where the forest had not been cleared to make farms, *Piptadenia africana* and *Lovoa brownii* are abundant. In swampy ground at the bottom of the valley, *Macaranga schweinfurthii* and *Pseudospondias microcarpa* are common trees; *Clinogyne leucantha* and *C. ugandensis* are common as undergrowth.

There are now about twenty people living in the valley and some of the forest on the northern side has been cleared again to make farms; many trees have been retained, including the big old specimens of *Canarium* and *Chlorophora* and some of the younger *Maesopsis eminii*; trees of *Ficus natalensis* have been planted and much of the ground is covered with plots of bananas and plantains, growing to a height of about 5 m., mixed with other crops such as *Coffea canephora*, *Capsicum frutescens*, *Dioscorea* spp. and *Calocasia antiquorum*. These banana gardens are on a dark red friable loam; most of the trees of *Chlorophora excelsa* growing in them are associated with termite mounds, as so frequently is the case in Uganda.

On the upper side of the banana gardens, near the edge of the grassland, much of the ground is paler in colour and lighter in texture than that on which bananas are growing. This land is used for growing other crops such as sweet potatoes and sorghum. Patches of ground which have been abandoned are colonized with a mixture of grasses, herbs and subshrubs such as *Brachiaria brizantha*, *Imperata cylindrica*, *Panicum maximum*, *P. trichocladum*, *Pennisetum purpureum*, *Setaria sphacelata*, *Indigofera arrecta* and *Laggera ovata*—species which are absent from the grassland above.

D. *Grassland on rocky slopes above the lake*

The ridge above the lake consists of an outcrop of quartzite; rounded boulders of the rock cover much of the top of the slope; the boulders have been cleared away from some places as if to allow room for cultivation. On some of the boulders there are signs of human influence: there are rectangular patterns of small shallow holes, such as are used for playing 'mweso', a game somewhat resembling draughts, which is very common in Tropical Africa; and there are shallow oval depressions like those in which corn is ground by Nilotic tribes in the north of Uganda and in the south of the Anglo-Egyptian Sudan—these are especially interesting, as the method of grinding is not used by the Baganda.

On the steeper slopes, where there is little soil between the boulders, the coarse grass *Eragrostis blepharoglumis* is a pure dominant, growing in large tufts with narrow hard leaves about 40 cm. long and with inflorescences rising to 60 cm. Where the slope is more gentle, there are smaller stones, chips of quartzite and light brown sandy soil between the boulders; in some places there is also an admixture of lateritic gravel and there is a thin layer of disintegrating ironstone on the upper surface of many of the rocks. In the places where there is more soil, there is a more mixed vegetation; *Eragrostis blepharoglumis* is still the dominant plant, but other species are common—the miniature sedge, *Fimbrostylis*

exilis, the subshrub *Coleus shirensis* and the grasses *Ctenium concinnum* and *Andropogon dummeri*. Large red-brown termite mounds are common and are covered with *Eragrostis blepharoglumis*. White and pale grey boulders, blotched with lichens, interspersed with the pale green leaves and inflorescences of *Eragrostis blepharoglumis*—such is the general effect of the rocky parts of the ridge. About one-third of the way down the slope, there is a stretch of flatter ground, free from rocks, covered with a sheet of glaucous *Hyparrhenia dissoluta*, like the hillside grassland of zone B. Below this zone, the ground again becomes rocky and steep, with exposed masses of quartzite and with tufts of *Eragrostis blepharoglumis* growing in the crevices, descending to the narrow strip of forest on the lake shore.

E. *Lakeside forest*

A narrow strip of forest, usually from 50 to 100 m. wide, stretches along the lakeshore at Nansagazi. The forest is low and irregular, with many breaks in the canopy overhead and many wide passages in the undergrowth, where the paths of the hippopotamus go down to the lake. The hippopotamus is the most important of the larger wild animals at Nansagazi: the buffalo and the antelopes have been killed or driven away in recent years, but there remain large numbers of hippopotamus. They make wide paths through the lakeside forest and through the valley forest of zone C; large pit traps may be seen in that forest, to catch them, for they do much damage to farms. The hippopotamus, in spite of their bulk and of their nocturnal habits, will travel far, and their characteristic double tracks may be followed right up into the hilltop grassland of zone A.

Yet it appears that it is not the hippopotamus, but the poor stony soil and the high winds which are responsible for the stunted growth of the lakeside forest; for the hippopotamus is an animal which grazes, rather than browses on trees. The largest trees are of *Canarium schweinfurthii*, but they are less than 20 m. high; most of the other trees are of quick growing species—*Anthocleista schweinfurthii*, *Maesopsis eminii*, *Polyscias fulva*, *Pseudospondias microcarpa*, *Ficus brachypoda*; the spreading *Ficus dawei* is common on the lakeside. There are many large shrubs in the undergrowth, such as *Trichalysia corbisieri* and *Dictyandra arborescens*; and there are many woody climbers. *Aframomon* sp. is common in the undergrowth.

Dense patches of *Pteridium aquilinum* are common on the upper side of the forest. *Harungana madagascarensis* and *Alchornea cordata* are common there, the latter species growing in dense thickets up to 5 m. high; it also forms thickets in some places on the lower side of the forest, where the pebbly shore slopes down steeply into the lake.

Nansagazi soils

No.	Zone	Situation	Character	pH	P	K	Ca
1	A	Hilltop grassland, *Loudetia kagerensis* dominant	Light brown sand mixed with lateritic gravel	4·0	1	1	0
2	A	Termite mound near sample 1, *Hyparrhenia diplandra* dominant	Light brown loam	4·5	Trace	1	Trace
3	C	Banana garden in valley	Red-brown loam	7·0	4	3	3
4	D	Soil among boulders, *Eragrostis blepharoglumis* dominant	Light brown sand mixed with small stones	4·0	1	Trace	0
5	D	Grassland below sample 4, *Hyparrhenia dissoluta* dominant	Red-brown fine sand	5·0	2	3	Trace
6	E	Lakeside forest	Fine brown sand mixed with stones	4·5	3	3	0

These soils, with the exception of sample 3, are like those of Bujumba—they are acid in reaction, poorly supplied in bases, and contain much fine sand. The soil from the banana garden in the valley, sample 3, is of a different type—it is neutral in reaction, rich in plant foods, heavier in texture and darker in colour.

Discussion on Nansagazi

This hillside is typical of most of the coast between Kampala and Jinja. The rainfall, though not so heavy as that on the Sese Islands, is good; the temperature is equable; and both the soil and the vegetation of this coast have affinities with those of the Sese Islands.

As at Bujumba, so also at Nansagazi, there are stretches of short, sparse, *Loudetia kagerensis* grassland; there is the same concentration of nutrients in and around termite mounds, there is the same sharp division between grassland and forest; some woody plants, such as *Harungana madagascarensis* and *Maesopsis eminii*, are common in both places.

But there are important differences: there is a greater diversity of species, both of grasses and of trees, at Nansagazi than at Bujumba; the cultivation at Nansagazi is concentrated on the valley, not on the hilltop as at Bujumba; and the cultivated soil at Nansagazi is much richer than at Bujumba—this richness is no doubt the reason why plantains, which grow poorly at Bujumba, grow well at Nansagazi, and the reason why the tree, *Chlorophora excelsa*, which grows well only on good soil (Thomas, 1942) is abundant at Nansagazi but is absent from Bujumba and from most other places on the Sese Islands.

Both at Bujumba and at Nansagazi, there is a blanket of ironstone near the hilltop: at Bujumba this blanket is overlain with a sufficient depth of soil for the hilltop to be cultivated, but at Nansagazi the soil is too shallow. There is no doubt that, if the soil were deeper at Nansagazi, the hilltop would be cultivated; for in places on these hilltops where the soil is deeper—and there is one such place close to the Nansagazi hill—farms of bananas, barkcloth trees, coffee and sweet potatoes do exist.

At Bujumba the best soil is in the valley, so farms are found there. It is interesting to note that this good soil which is under farms or forest extends up the slope facing north, away from prevailing breeze, but is absent from the slopes facing south, which are subject to much wind. Nansagazi is so close to the equator that there can be little difference in the incidence of sunlight on northern and southern slopes. It is possible that geological factors are involved but, as will be seen from the description of the catenas at Mpambire and at Kawanda, it is often seen that the northern slopes of the hills are more forested than the southern and that wind does appear to be an important factor in controlling the vegetation.

MPAMBIRE

The hillside at Mpambire is situated at 0° 12′ N. and 32° 12′ E. It consists of a slope over 1 km. long descending southwards from a flat-topped hill down to the valley of the river Nakyetema; this valley is filled with papyrus swamp about 1 km. wide; from the top of the hill to the level of the swamp there is a vertical fall of about 100 m. The average rainfall of the area seems to be about 1300 mm. a year.

The Mpambire catena (Fig. 5) comprises four well-defined belts, easily distinguished to a distant view:

    A. Hilltop grassland.

    B. Elephant grass and cultivation complex.

    C. Evergreen forest.

    D. Papyrus swamp.

A. *Hilltop grassland*

The zone covers the narrow flat top of the hill, which is only about 50 m. wide, and the first 100 m. of the upper slopes of the hill. It consists of coarse tufted grassland with few woody elements. When the grass has not been burnt for some months, it forms a dense mass of leaves and stems, nearly 1 m. high, above which protrude the taller
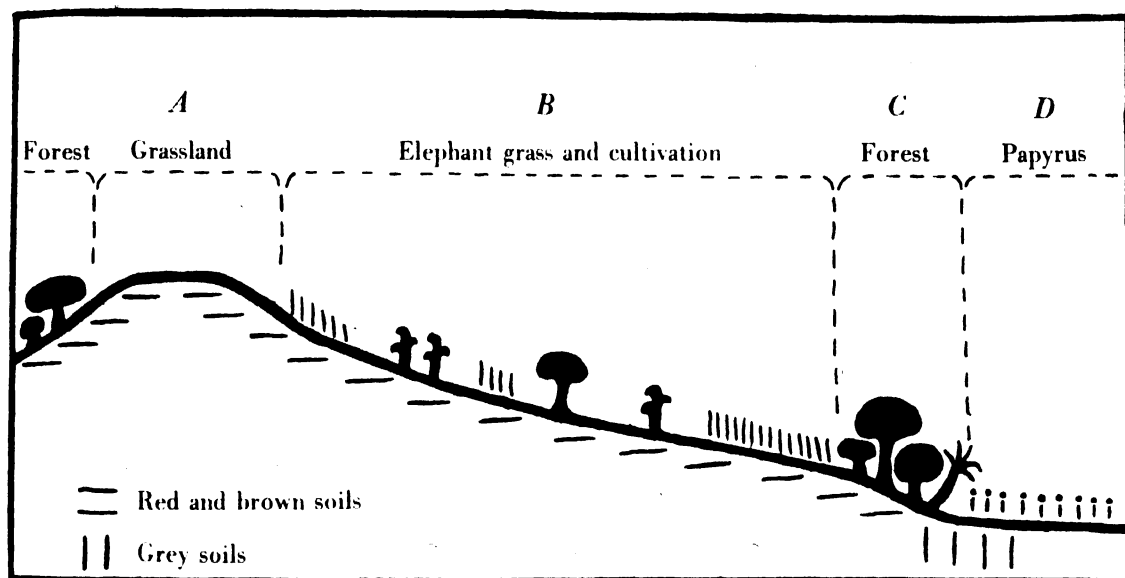
Fig. 5. Diagram of catena at Mpambire.

flowering stems of some species. *Hyparrhenia diplandra* is the dominant species and its coarse yellow-green leaves and brownish inflorescences, which reach a height of 2 m., determine the general appearance of the grassland. *Beckeropsis uniseta* is fairly common and there are occasional specimens of *Hyparrhenia cymbaria*; the panicles of both of these species attain to heights of more than 2 m. *Cymbopogon afronardus* is abundant; its tufts of glaucous leaves, rather shorter than those of *Hyparrhenia diplandra*, are intermixed with them; *Imperata cylindrica* is common. Smaller species are also intermingled, notably a small form of *Hyparrhenia filipendula*, growing in erect tufts to a height of about 1 m., and *Panicum fulgens*, with fine weak stems which are scandent among the larger grasses.

When the grassland has been burnt, its appearance is very much altered. The tangle of leaves and stems disappears and much bare ground is revealed. The clumps of the larger species, such as *Hyparrhenia diplandra* and *Cymbopogon afronardus*, are often as much as 0·5–1 m. apart; between them are tufts of smaller grasses, usually 10 cm. or more apart and, as these grasses are erect in growth, the rest of the ground is uncovered.

Some of the smaller grasses are more precocious in flowering than the large ones, and therefore are easily recognized a few weeks after the grassland has been burnt; such grasses are *Andropogon dummeri*, *Digitaria maitlandii* and a small form of *Setaria sphacelata*. All of these species grow in small tufts and their inflorescences are only about 50–70 cm. high, so that they are obscured when the coarse grasses have made their full growth.

A few subshrubs are common in the grassland, notably *Lippia adoensis*, *Indigofera emarginella* and *Guizotia schultzii*. There are a few woody elements—some groups of *Gardenia jovis tonantis*, in the form of fire-scarred bushes 2 m. high; and, near the lower edge of the zone, there are specimens of *Grewia mollis* and *Acacia holstii*, both species growing as small trees about 3 m. high. But most of the grassland is open.

On the northern side of the hill there are more trees. Near to the top there are small trees of *A. holstii* and *Combretum gueinzii*, species typical of woodlands in dry conditions. Below them there are larger trees, such as are found in wetter areas—*Albizzia coriaria*, *A. zygia*, *Lovoa brownii*—and these are so close in places as to form patches of forest 15 m. high.

B. *Elephant grass and cultivation complex*

This is the widest zone in the catena, occupying a belt about 600 m. wide and covering all the slope of the hill with the exception of the narrow strips of grassland at the top and of forest at the bottom. This complex is of varied composition: there are patches of tall dense elephant grass (*Pennisetum purpureum*), patches where the grass is shorter and sparser, patches where the ground is covered with weeds and grasses after cultivation has been abandoned, patches of annual crops such as cotton, patches of perennial crops such as bananas; the area is intersected with paths and dotted with houses. Elephant grass is the species to which this land reverts soon after it has been abandoned, and is the plant most typical of the zone, although it occupies only about one-quarter of the area at the present time. 'Thicket' seems to be the best term for the *Pennisetum purpureum* association; the growth of the grass is tall and dense, and the bamboo-like stems persist for two or three years, if unburnt, so that the term 'grassland' does not describe the formation.

The hilltop grassland ends abruptly, above an outcrop of granite. Below this outcrop there is a sudden fall of 1 m. in the ground level, at the top of the land which has been recently cultivated for, as it is natural to dig the soil with a hoe downwards, there has been a movement of soil downhill. Little of this upper part of the elephant grass zone is now in cultivation, as it has lost much of its fertility.There are some patches of sweet potatoes and cassava, crops which can be cultivated on exhausted land, but much of the land has been abandoned. This abandoned soil is red in colour, mixed with stones and rock fragments, and very hard on the surface—on some plots which obviously have been abandoned for many months there are bare patches of soil, not yet colonized by any plants.

The first plant to colonize the poor soil of abandoned plots is *Bidens pilosa*; it is followed by other annual plants of the same family (Compositae)—*Ageratum conyzoides* and *Erigeron linifolius*. Then grasses appear—*Sorghum verticilliflorum*, *Rhynchelytrum repens* and *Panicum trichocladum*, intermixed often with subshrubby plants such as *Guizotia schultzii* and *Indigofera arrecta*, and the twining *Cissampelos mucronata*. These species in turn are succeeded by tall perennial grasses—*Beckeropsis uniseta* and *Hyparrhenia rufa*; finally, a year or two after the land has been abandoned, *Pennisetum purpureum* becomes

established and gradually the land reverts to a thicket of this species; but it does not grow so dense or so tall as the elephant grass on richer soil near the bottom of the slope and is seldom more than 3 m. high.

The poor eroded land extends over 200 m. down the slope to the first houses. Some of the soil near the houses is good, with flourishing coffee trees close to the kitchens, on spots where rubbish has been thrown. But a great deal of the land above the houses has lost its fertility and the plots of bananas are being abandoned because they are in poor health.

The main zone of cultivation lies below the first line of houses, extending for about 240 m. down the hill. There are extensive plots of bananas, covering at least one-third of the ground; there are plots of perennial food crops, sweet potatoes and cassava, and plots of annuals such as cotton (*Gossypium hirsutum*) and beans. There are also patches of land recovering from cultivation and in the process of reverting to elephant grass.

Ficus natalensis, whose bark is used to make a rough cloth, is the common tree in this zone, growing to a height of about 8 m.; specimens have been planted in many of the banana gardens and in patches around the houses. A few clumps of sugar cane and a few orange trees and mango trees are planted near the houses; and mango trees are growing on land which has been abandoned, for this species is resistant to fire. Small patches of coffee (*Coffea arabica* and *C. canephora*) also are grown. One single tree of *Chlorophora excelsa* grows by a termite mound near an old house site. In addition to food plants, small patches of other useful species are to be seen—a large clump of *Sansevieria* sp. grown for fibre; plants of *Kalanchoe* spp., grown for medicines; and specimens of the small soft-wooded tree *Vernonia amygdalina*, which grows spontaneously here, are retained because an infusion of their leaves is used to cure malaria. The fruit trees and medicinal plants are in small amounts: it is the elephant grass and the banana which are the most abundant plants in this zone.

There are several weeds which are very common in the cultivated land. The quick growing annual composites—*Galinsoga parviflora*, *Bidens pilosa*, *Senecio discifolius* and *Ageratum conyzoides*—all of which grow rapidly and seed abundantly, need frequent cultivation if they are to be controlled. The perennial *Commelina nudiflora* is difficult to eradicate, as its succulent stolons cannot be killed by exposure to the sun and must be burnt or buried. *Imperata cylindrica* soon invades abandoned land and is mixed with the elephant grass in this zone; but this grass, which is such a pest in the East under the name of lalang, is easily killed in Uganda by repeated hoeings. *Digitaria scalarum*, which also is abundant here and which also has succulent rhizomes, is much more difficult to kill and is a 'couch grass' of the worst type; its control is a major problem of cultivation on this zone.

Soil erosion is not marked in the centre of the cultivated zone, being much less than on the poorer, steeper, slopes higher up; in fact, any soil washed down is retained in this zone. But erosion does take place in three places—first, on the bare ground near the houses; secondly, on the paths running down to the waterholes at the base of the hill; and thirdly in the ditches, which are sometimes nearly 1 m. deep, cut down the sides of cultivated plots to prevent invasion by the rhizomes of *Digitaria scalarum*. As these ditches are seldom very long, the soil washed down them is held up by patches of elephant grass below. The soil is of a type resistant to erosion and is typical of that covering much of the slopes in the south of Buganda; it consists of a red-brown loam, about 20 cm. deep, over a red clay.

There are no houses near the bottom of the slope, the lowest being nearly 200 m. from the forest edge. The farms extend about 100 m. below the houses, but the remainder of the slope is under a dense belt of elephant grass. This zone does not seem to have been disturbed for some years and forms a thick mass of stems, up to 4 m. or more in height: *Imperata cylindrica* is abundant but is obscured when the elephant grass has grown: in places where there is a break in the canopy of elephant grass, such as at the edge of paths, *Guizotia schultzii* is common.

C. *Evergreen forest*

There is a great contrast between the tall dark green of the forest and the lighter green of the elephant grass thicket and, to the distant view, there is an abrupt line of demarcation between them. Inspection of the forest edge shows that the zone of transition between the two is a narrow one, less than 10 m. in width. The forest is encroaching on the elephant grass. *Acanthus arboreus*, a coarse shrub which attains a height of 5 m., is the pioneer species and is dominant at the forest edge. The smaller, subshrubby, *Acalypha ornata* is common there also. The thickets of *Acanthus* are colonized by tree species—the soft-wooded, very quick growing *Polyscias fulva* is the most common, and this in turn is replaced by other, more hard-wooded, trees.

In many places the canopy of the forest has been broken by the felling of trees for timber and it seems that many of the better trees have been removed; at the present time there is a mixture of trees, a high proportion being of species of little value. *Pseudospondias microcarpa* and *Ficus capensis* are two of the most common species: *Polyscias fulva*, *Croton macrostachys*, *Pycnanthus kombo*, *Piptadenia africana*, *Albizzia zygia* and *Maesopsis eminii* are all common. These species form the canopy of the forest at a height of about 15–20 m. The liane, *Landolphia florida*, is a common climber over the trees, especially near the upper edge of the forest. Smaller trees occur in the second storey— notably *Tarenna pavettoides*, *Ficus exasperata*, *Voacanga obtusa* and *Euphorbia teke*. Seedlings of *Phoenix reclinata* and *Teclea nobilis* are common in the shrub layer, though few large specimens of *Teclea* are present; it is probable that they have been cut out, as their wood is tough and useful.

In those parts where the canopy has not been broken, there is dense shade; in such places the coarse forest grass *Leptaspis cochleata* is dominant, growing to a height of about 50 cm. In other parts of the forest, where more light reaches the ground, other species are common—*Palisota schweinfurthii*, with its big rosettes of leaves, *Forrestia* sp. and other members of the *Commelinaceae*, *Piper umbellatum*, *Clinogyne ugandensis* and *Renealmia* sp. (aff. *R. africana*). *Culcasia scandens* is very common both as a climber on the trunks of the trees and also as a creeper over the ground. *Polypodium iridiodes* is an abundant fern, growing on the trunks and branches of trees and also at ground level.

Although there are many plants growing on the ground, yet they do not give a complete cover over the soil; a great deal of it is littered with fallen leaves which form a loose layer about 2–3 cm. thick—those at the top are undecomposed, those below are rotting and becoming embedded in the soil. The soil itself is light brown in colour, sandy in texture and very permeable, as is usual with the soils of forests in Uganda. Small twigs and branches are common on the surface, but many are gathered for firewood by the people living on the hill above.

Not only does the forest supply timber and fuel, but it is also the source of the water

supply. A path leads down to a permanent water-hole near the lower edge of the forest, at a place where a spring seeps out just above the level of the swamp. In the area, where the ground is permanently waterlogged, *Ficus congensis* is the dominant tree together with a few palms (*Phoenix reclinata*); and the ground is covered with a thicket, about 2 m. high, of *Clinogyne leucantha*. As the forest lies along the edge of the swamp, the air inside it is always moist, and mosquitoes are very numerous, even in the daytime.

The lower edge of the forest appears to be slowly creeping into the swamp. The palm, *Phoenix reclinata*, is abundant, forming groups of stems up to a height of 6 m. Many low trees grow between the palms—notably *Bridelia micrantha*, *Alchornea cordifolia*, *Macaranga schweinfurthii* and *Neoboutonia melleri*—forming a mass of low foliage below the crowns of the palms.

D. *Papyrus swamp*

The bottom of the valley is filled in with papyrus swamp which, when viewed from above, appears as a horizontal expanse nearly 1 km. wide and several kilometres in length, stretching along the course of the R. Nakyetema; there is a considerable flow of water down this river and there is a strong current below the papyrus in the centre, where it appears to be floating high above the true land surface. *Cyperus papyrus* is the dominant species, forming a dense mass of stems about 3·5 m. high, crowned with the finely branched globular inflorescences. In the centre of the swamp there are few other species mixed with the papyrus: in places where the growth is not very dense, the fern *Dryopteris striata* spreads its rhizomes among the base of the stems and its fronds ascend to a height of about 1 m.

A road crosses the swamp and, where an opening has been cut in the papyrus, there is a greater diversity of plants. The coarse subshrubby *Triumphetta macrophylla* is common, and so is the small swamp grass *Leersia hexandra*; in the ditches the mauve-flowered *Nymphea capensis* is abundant. Woody elements are rare except near the edges, where *Ficus congensis* is common: there are two small groups of the same species, growing to a height of about 6 m. in the middle of the swamp, which show up darkly from among the paler level expanse of papyrus.

Mpambire soils

No.	Zone	Situation	Character	pH	P	K	Ca
1	A	Hilltop grassland	Brown loam	5·5	2	1	2
2	B	Abandoned farmland at top of zone	Red-brown loam, very hard	5·0	1	2	1
3	B	Elephant grass near bottom of zone	Dark brown sandy loam	5·5	1	1	2
4	C	Evergreen forest	Light brown sandy loam	5·0	2	2	1
5	D	Papyrus swamp	Dark brown spongy	5·0	1	4	1

All of these are acid, and none of them are very rich in plant nutrients.

Discussion on Mpambire

The catena at Mpambire, both as regards vegetation and soil, is typical of the area in which it lies. Hilltop grassland, elephant grass thicket and cultivations, evergreen forest and papyrus swamp—these zones are repeated on hill after hill. In some places the lower zones are modified—in some places the forest is the lowest zone of the catena, for in smaller valleys there are no papyrus swamps; in other places the forest has been cut out and the elephant grass—cultivation complex stretches down to the edge of the swamp.

And, in the region to the west of Mpambire, grassland such as that on the hilltop comes far down the sides of the hills and covers most of the landscape.

The soils are not rich—they are good enough to support the growth of elephant grass and of bananas, but neither species grows so luxuriantly as on some of the better land to be found to the east of Kampala and, as mentioned above, the elephant grass regenerates slowly on the abandoned farmland. But there is not a very dense population around Mpambire and land can be left long enough under a fallow of elephant grass for it to recover its fertility, which is not merely a question of the supply of nutrients but also depends on the structure of the soil (Martin, 1944).
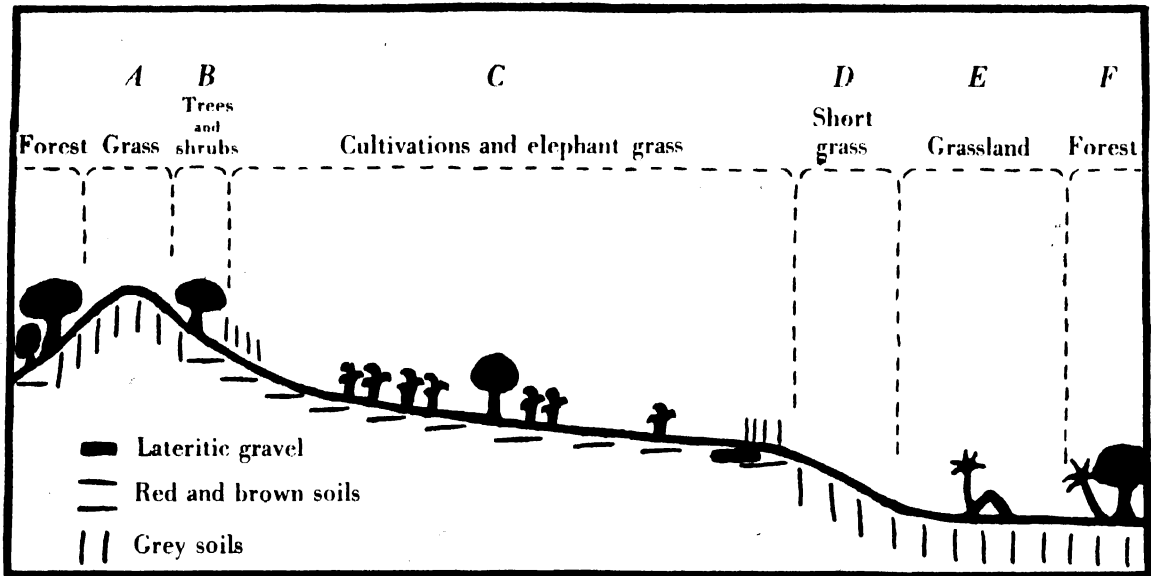
Fig. 6. Diagram of catena at Kawanda.

KAWANDA

The hillside at Kawanda is close to the Agricultural Research Station and is situated about 0° 20′ N. and 32° 33′ E. The top of the hill is composed of a ridge of quartzite, reaching an altitude of about 1200 m.; the ground slopes south down to the valley of the small river Mayanja. There is a ring of higher hills around Kawanda, a fact which may explain why it has a rainfall less than is usual in the district; in some years the total is less than 1000 mm. and it seems that the average is only about 1100 mm.

Six distinct zones can be seen in this catena (Fig. 6 and Pl. 3, phot. 2):

A. Hilltop grassland.
B. Belt of trees and shrubs.
C. Elephant grass and cultivation complex.
D. Short grass and cultivation complex.
E. Valley grassland and termite mound complex.
F. Riverine forest.

A. *Hilltop grassland*

This zone is confined to the narrow top of the hill and to about 25 m. of the upper steep slope. The ridge of the hill is an outcrop of quartzite and there is much of the bare rock exposed; in some places there is up to 10 cm. of grey sandy soil, mixed with stones

and containing a mass of roots. The vegetation is of grassland, with scattered specimens of *Entada abyssinica*, small dwarfed trees less than 3 m. in height.

The grass *Cymbopogon afronardus* is the dominant species, growing in large tufts as much as 1 m. apart, and its glaucous leaves give a general grey colour to this zone. Other grasses are common, notably *Hyparrhenia filipendula* and *H. diplandra*; they, like the *Cymbopogon*, reach a height of 1 m. or more. In between the tufts of these large grasses are the much smaller tufts of *Microchloa kunthii*. Some erect subshrubby species—*Lippia adoensis*, *Vernonia campanea* and *V. grantii*—are mixed with the grasses. When the vegetation is fully grown, the ground appears to be well covered; yet, after the fires which occur once or twice a year, most of the surface is exposed.

On the north side of the hill, where the ground is equally steep and rocky, there is a small belt of relict closed evergreen forest, growing to a height of about 12 m. *Albizzia zygia*, *Sapium ellipticum* and *Chrysophyllum* sp. are the most common trees: *Acacia pinnata* and *Grewia* sp. (aff. *G. platyclada*) are common woody climbers; *Argyromuellera macrophylla* and *Coffea eugenioides* are shrubs in the undergrowth. The persistence of this patch of forest is due to two factors: first, that the ground on which it grows is too poor and too stony for cultivation and, secondly, that it is protected by the hill from the full force of the fires which sweep up the south side of the hill during the dry seasons as far as the top but which only scorch the outside of the forest sheltered below on the north side.

B. *Belt of trees and shrubs*

The bottom of the grassland merges into a belt in which bracken fern (*Pteridium aquilinum*) is dominant, mixed with tufts of *Hyparrhenia diplandra*, both species growing to a height of 2 m. There are many suckers of *Albizzia zygia*, growing from the roots of larger trees, which reach a height of 15 m.; there are several of these trees at a distance of about 100 m. from the top of the hill, together with smaller trees of other species—*Entada abyssinica* and *Morinda lucida*.

Under the trees, there is a thicket of shrubs about 3 m. high, *Flueggea virosa*, *Acalypha neptunica* and *Vernonia amygdalina*, together with a few seedlings of *Phoenix reclinata*. This belt of trees and shrubs is narrow and it merges into the top of the elephant grass zone, which contains many coppiced plants of *Albizzia zygia*.

C. *Elephant grass and cultivation complex*

This zone starts at a distance of about 150 m. from the hilltop and, at its upper edge, it contains many coppiced *Albizzia zygia*. The elephant grass forms a thicket about 4 m. high, with much *Imperata cylindrica* growing in admixture with it; when the elephant grass is fully grown, it obscures the *Imperata* but, after it has been burnt, the zone becomes a mass of white inflorescences of *Imperata* followed by the precocious leaves, up to 1 m. in height, for *Imperata* is much quicker both in leaf growth and in flowering than is *Pennisetum purpureum*.

This zone is used for occasional cultivation of crops—cotton, sweet potatoes and cassava—which do not require a high fertility; the soil is mostly a brown clay, redder in patches, with occasional red-brown termite mounds.

The uppermost houses on the hillside are about 300 m. from the hilltop. Below the houses there are many gardens of bananas and plantains (*Musa sapientum* and *M. paradisiaca*) which are, in fact, the dominant plants in the centre of the hillside, covering

more than half the ground. There are plots of other crops—cotton, sweet potatoes and cassava—and smaller amounts of maize, pineapples, herbs and medicinal plants; and there are several barkcloth trees (*Ficus natalensis*). Practically all the ground is culti- vated, but grasses are growing on a few untilled patches—*Panicum maximum*, *Imperata cylindrica* and *Digitaria scalarum* (the last is a bad weed here). The most common ephemeral weeds are *Bidens pilosa*, *Euphorbia heterophylla* and *Digitaria velutina*.

On account of the pressure on land, little of it can be left to recover under a fallow of elephant grass, which would quickly colonize abandoned plots. But, in spite of the fact that the land is sloping and is cultivated almost continuously, there is not much erosion. For one thing, the soil is of a type which does not erode badly: it is a brown loam, about 20 cm. deep, overlying a red clay which has little variation in texture or colour down to a depth of several metres. Devices to control erosion are part of the indigenous system of farming: silt pits are made in the banana gardens to hold up water in places where it comes down the hillside; and, when erosion starts on the paths which run down the hillside to the water-holes, bananas are planted in them, suckering to form large clumps which hold up the soil and prevent the formation of gullies.

At the top of this zone and also at the bottom, there is a belt used for occasional cultivation, in which the resting land becomes colonized by *Imperata cylindrica* and *Pennisetum purpureum*.

D. *Short grass and cultivation complex*

The houses, the banana gardens and the red-brown soil extend to a distance of about 800 m. from the hilltop: then the houses become fewer, the banana gardens poorer and the soil alters in character—it is grey and sandy, overlying a brown subsoil. This zone is used for cultivation of crops like those at the top of the elephant grass belt—cotton, sweet potatoes and cassava, together with some soya beans.

After crops of sweet potatoes and cassava, the land is left to regenerate: it becomes colonized by *Bidens pilosa*, *Erigeron linifolius* and *Sida rhombifolia*, and then by grasses— *Digitaria scalarum* and *Panicum maximum*, which are kept grazed. There are clumps of *Pennisetum purpureum* around the anthills in this area.

The zone, which is about 250 m. wide, is on a steep slope, steeper than that of zone C, and falls down to the almost flat bottom of the valley, which is covered with short grass- land, on whose upper parts there are low ditches and mounds—evidence that patches of it have been cultivated in the past.

E. *Valley grassland and termite mound complex*

This grassland, like that on the hilltop, has a predominant grey hue, for *Cymbopogon afronardus* is dominant at the bottom of the hill as well as at the top. The soils in the two zones are very different in texture—that on the hilltop is very sandy and very shallow, while that in the valley bottom is a deep, pale grey, sandy clay. The *Cymbopogon afronardus* grows in large tufts of glaucous leaves, just as in the top of the hill; and in this zone, too, it is intermixed with large tufts of *Hyparrhenia diplandra*.

This valley grassland is used as pasturage for a number of cattle, and is fairly heavily grazed; but the cattle avoid both *Cymbopogon afronardus* and *Hyparrhenia diplandra*, which grow in large tufts, usually about 0·5–1 m. apart, raised above the general level of the ground, and feed on smaller grasses—notably *Hyparrhenia filipendula*, *Brachiaria*

Phot. 1. Nansagazi catena. Rocky grassland (zone D) and, in the distance,
a strip of lakeside forest (zone E).

Phot. 2. Kawanda catena. General view from hilltop showing belt of trees and shrubs
(zone B), elephant grass and cultivation complex (zone C), valley grassland (zone E)
and riverine forest (zone F).

Phot. 3. Kawanda catena. Valley grassland (zone E). Clumps of *Cymbopogon afronardus*, with smaller grasses between; to the right, groups of *Phoenix reclinata*, growing on termite mounds; to the left, riverine forest (zone F).

Phot. 4. Kakinze catena. A plot of cotton planted in a clearing of woodland (zone C); the large tree left is *Combretum gueinzii.*

soluta and *Eragrostis mildbraedii*—which grow between; *Imperata cylindrica* also is common in this grassland, but its leaves are eaten only when they are young (Pl. 4, phot. 3).

The valley bottom is not quite flat. On the higher patches, the coarse grasses are less frequent and there is more of a short turf of the smaller species, *Hyparrhenia filipendula* being dominant; in some higher places there are groups of *Acacia holstii* bushes; it is probable that there used to be cattle kraals here, for this *Acacia* is often associated with old kraal sites. At the present time, the cattle are kraaled on the side of the valley, in zone D.

There are hollows in the valley, places where the ground is waterlogged or even flooded for part of the year. *Miscanthidium violaceum* is locally dominant in these wet parts, forming a mass of narrow, erect, sharp-edged leaves 3 m. high, and its inflorescences reach a height of 4 m. In some places another tall grass, *Loudetia phragmitoides*, is associated with the *Miscanthidium*, and the subshrubby *Dissotis macrocarpa*, with large purple flowers, often grows in admixture with it. The ground in the swampy parts is heavily trampled: in some hollows where the water lies, the clumps of grasses are on mounds 0·5 m. high, with deep tracks between.

Large spreading grey termite mounds are common along the valley. *Phoenix reclinata* is the dominant tree growing actually on them (not around the base, as in the case of the trees around the termite mounds at Bujumba) and *Erythrina tomentosa* is sometimes associated with it. The shrub, *Flueggea virosa*, is also common on the mounds; *Hoslundia opposita* and *Acanthus arboreus* grow near the base of the mounds. *Pennisetum purpureum* is abundant on the mounds growing near the side of the valley, but is absent from those near the centre.

F. *Riverine forest*

A strip of evergreen forest, about 100 m. wide, runs down the centre of the valley along the course of the Mayanja river. There is a considerable flow of water in rainy weather; in the dry season there is little flow above ground, but there is always water in shallow holes along the water course and the ground is waterlogged up to the surface. In some places the wet ground extends beyond the boundary of the forest and there is a thin belt of *Cyperus papyrus* outside the trees; the stems of this papyrus are shorter than those of the plants in the swamp at Mpambire, being about 2·5 m. high.

The edge of the forest beside the grassland is a thicket of *Acanthus arboreus*, *Aframomum* sp., *Alchornea cordifolia* and *Bridelia micrantha*. Behind this thicket there is a belt of *Phoenix reclinata* palms, growing to a height of about 10 m. There are palms growing also in the centre of the forest among a mass of other trees—*Erythrina excelsa*, *Pseudospondias microcarpa*, *Ficus congensis*, *Schefflera urostachya* and *Sapium ellipticum*. The canopy of these trees, together with woody climbers, casts a fairly dense shade; *Euphorbia teke* grows in the undergrowth—it is strange that this small succulent tree should be characteristic of these dense swampy forests. The climbing *Culcasia scandens* is common both as a climber on the trees and also spreading over the ground; ferns are common, especially *Polypodium iridiodes* as an epiphyte and *Nephrolepis biserrata* on the ground. *Cyperus renschii* is common in the places where much light reaches ground level. The surface soil is dark brown, swampy, with a mass of roots spreading over its surface; in the centre of the forest this swampy soil is deep, but at the sides it forms a very thin layer over grey sandy clay, like that of the grassland.

Kawanda soils

No.	Zone	Situation	Character	*p*H	P	K	Ca
A	1	Hilltop grassland, *Cymbopogon afronardus* dominant	Grey, with much coarse sand and small stones	5·0	2	2	1
B	3	Top of elephant grass zone	Brown clay loam	6·0	1	2	2
C	3	Good banana garden	Red-brown loam	6·0	2	4	2
D	4	Cotton plot	Brown sandy loam	5·5	1	1	2
E	5	Valley grassland, *Cymbopogon afronardus* dominant	Pale grey sandy clay	5·0	1	2	0
F	6	Riverine forest	Grey-brown clay mixed with decaying roots and leaves	5·0	1	1	1

The most interesting feature of the soil is the fact that both at the top and bottom of the slope, where *Cymbopogon afronardus* is dominant, there are grey soils, poor in plant nutrients; in the middle of the slope, where the houses and banana gardens are situated, the soil is redder and richer. This zonation of soils, grey on the hilltops, red on the sides of the hill and grey in the valleys, is described by Martin and Griffith as being typical of much land in Buganda (Martin & Griffith, 1940). There seems to be little lateritic ironstone or lateritic gravel on this hillside, with the exception of some gravel at one place near the bottom of the elephant grass zone: yet, on the neighbouring hill where the Agricultural Research Station is situated, there is a great deal of lateritic gravel in large patches both on the top and on the sides of the hill.

Discussion on Kawanda

This catena, or modifications of it, is typical of much of the land close to Kampala; there is a great pressure on this land, for not only is there dense settlement but also many crops, in addition to coffee and cotton, are grown for sale; the sweet potato is a very important one, for it can be grown on land whose fertility is not very high, such as can be seen at the top of the elephant grass zone and in the zone of poor soil just above the valley grassland.

Many of the hills are lower than Kawanda, without the central ridge of quartzite: the houses and banana gardens are concentrated on the rounded tops of such hills. In many other cases, all the riverine forest has been cut out and the valley bottom is covered with grassland; if the site is well drained, *Cymbopogon afronardus* is the dominant species but, in many valleys where the land is waterlogged for part of the year, *Miscanthidium violaceum* is dominant.

The valley grasslands are important, for they are the areas which are used for grazing: elephant grass is palatable and nutritious but, as a rule, cattle are not allowed to graze on it, as the species is soon killed out by hard grazing and is replaced by poorer grasses, such as *Imperata cylindrica* and *Digitaria scalarum*. When land is cleared from elephant grass, much labour is needed to dig out its woody root stocks; but this labour is much less than that required to clean the land of the rhizomes of *Imperata* or *Digitaria*; and the deep and extensive root systems of elephant grass appear to restore soil fertility better than those of other grasses. It is on account of the beneficent action of elephant grass which regenerates on abandoned farms and restores their fertility that the land around Kampala has been able to carry a heavy population for a long time.

It is probable that there has been dense settlement at Kawanda over a long period; on a hill across the valley there is the tomb of the Kabaka Suna, who died in 1857. The

land may not have been continuously settled, as village sites were abandoned when soil fertility was unduly depleted, or when there was an epidemic of plague.

In former times, the hill would be more or less self-supporting; the foodstuffs grown on the hill were consumed there and the mineral residues returned to the soil. But now there is a drain on the land, for not only is it more intensely cropped and has less opportunities to regain fertility under elephant grass leys, but also every pound of cotton or sweet potatoes that is sold will mean the loss of more plant nutrients.

Actual soil erosion does not seem to be acute under the present conditions of intensive cropping. There is, no doubt, a gradual movement of soil down the hill, but it is compensated by the residues of foodstuffs, of firewood and of the droppings of stock which are brought up near the houses. The valley soil is grey; the soil above is red-brown or brown so that, if it were washed down, it could be easily detected; no sign of the deposition of such soil can be seen. Furthermore, the actual shape of the valley, which is typical of many other valleys in the neighbourhood, seems to indicate that soil is not being washed down to the bottom; for the slope is not even—it falls rapidly from the hilltop down to the zone of cultivation and settlement, where the slope is gentle; and from the base of this zone, it falls steeply down to the valley grassland.

As there is such pressure on land, most of the game animals have been driven away; there seem to have been no buffalo at Kawanda for the last twenty years, but reedbuck still come there. Monkeys and tree hyrax are still to be heard in the narrow strip of riverine forest; and the large edible rat is common in the patches of elephant grass.

KAKINZE

The hillside at Kakinze is situated at 0° 55′ N. and 32° 28′ E.: it slopes from an outcrop of gneissose granite at the top of the hill down to a valley about 60 m. below and about 1400 m. to the north. The average annual rainfall is probably about 1100 mm.

There are four well-marked zones (Fig. 7):

A. The outcrop of granite.
B. Banana gardens.
C. Woodland with patches of cultivation.
D. Valley grassland.

A. *The outcrop of granite*

There are large rounded bare masses of rock, with grey sandy soil in the fissures between them. The smallest crevices, where there is little soil, are colonized by *Cyanotis lanata* and *Fimbrostylis exilis*. Larger cracks contain a mixture of subshrubs about 50 cm. high—*Coleus forskohlii* and *Astrochlaena malvacea*—and small grasses—*Sporobolus festivus* and *Brachiaria kotschyana*. The largest hollows, where the soil is deepest, are covered with a dense mass of the grass *Loudetia arundinacea*, growing to a height of 1·5 m.: other tall grasses—*Hyparrhenia filipendula* and *H. cymbaria*—are present in small amounts.

B. *Banana gardens*

The remains of tree species typical of woodland country in Uganda—*Combretum gueinzii, C. binderianum, Albizzia coriaria* and *Grewia mollis*—are to be seen close to the base of the rocks, but they have been ringbarked and killed to make place for cultivated crops. In some places bananas are planted close to the rock; in others there are

3-2

patches of other crops— sweet potatoes, sugar cane and cotton—growing on grey sandy soil between the rocks and the bananas: and land which has been abandoned from cultivation is colonized first by *Imperata cylindrica* and then by *Pennisetum purpureum*.

Banana gardens cover most of the upper slopes of the hill, forming a belt about 300 m. wide, very distinctive on account of its intense green, especially in dry seasons when the leaves of wild trees and grasses are parched and dull in colour. Most of the bananas (including plantains) are grown in large clumps at irregular spacings of 3–5 m.; the average height, to the top of the leaves, is about 4 m. There are many houses in this zone.

Occasional trees stand out among the bananas; *Chlorophora excelsa*, with its dark spreading crown, is the tallest; *Ficus gnaphalocarpa* forms spreading rounded trees about 8 m. high; *F. natalensis* and *F. brachypoda*, species which are cultivated for barkcloth, form dense crowns of glossy leaves 6 m. high; and there are a few erect trees, also about 6 m. high, of the yellow-flowered *Markhamia platycalyx*, a species cultivated to supply poles.
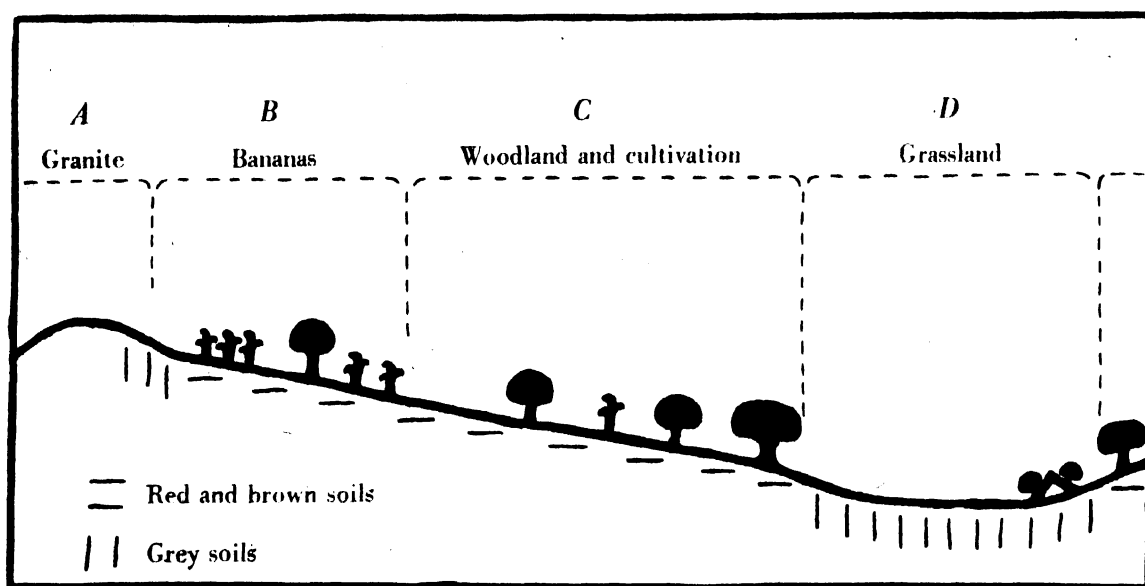
Fig. 7. Diagram of catena at Kakinze.

Patches of other crops are intermixed among the bananas—shrubs of coffee (*Coffea canephora*) near the houses, plots of sweet potatoes, of cotton and, in a few places, of cassava. The grasses *Imperata cylindrica* and *Panicum maximum* soon colonize uncultivated ground and are succeeded by *Hyparrhenia rufa*, *H. cymbaria* and *Pennisetum purpureum*. And there are also small areas of relict woodland, not now cultivated, with small trees of *Acacia holstii*, *Grewia mollis* and *Combretum binderianum*.

C. Woodland with patches of cultivation

The second zone, in which the banana is the dominant plant, grades into the third in which, while there are many dwellings, many banana gardens and many other patches of cultivation, yet more than half the ground remains under a cover of woodland. This zone is a wide one, covering over 800 m. on the lower slopes of the hill.

The woodland which remains is mostly of a low, open type; most of the trees have a

height up to 8 or 10 m., and the trees are frequently 8–10 m. apart. Many species are represented—*Albizzia coriaria*, *A. zygia*, *Combretum binderianum*, *C. gueinzii*, *Vitex fischeri*, *Acacia holstii*, *Gymnosporia senegalensis*, *Stereospermum kunthianum* and *Pavetta crassipes* are some of the most common ones; the last four species are shrubs or trees up to 4 m. high.

Beneath the trees there is an abundance of grasses; *Imperata cylindrica*, *Panicum maximum*, *Hyparrhenia filipendula*, *Setaria sphacelata*, *Brachiaria brizantha* and *Sporobolus pyramidalis* are some of the common species. This zone is much used for grazing—the presence of *Sporobolus pyramidalis* is usually a sign of hard grazing; and, while the grasses grow to a height of 1·5 m. in the rainy weather, yet by the end of the dry seasons they have been eaten down close to the ground.

The intensity of settlement and cultivation is higher at the top of the zone than at the bottom. There is near each house a cleared area, part of which is planted with bananas; they grow fairly well. Other parts of the cleared land are used for root crops—sweet potatoes and cassava—and annual crops such as cotton, beans, simsim and finger millet. The land is not wholly cleared for some of the cotton plots—the smaller trees are dug out and the larger ones are either cut down or are left standing; the ground is dug over and, after the crop has been grown and gathered, the plot is abandoned. Such plots are soon colonized by perennial grasses, notably *Digitaria scalarum* and *Imperata cylindrica*, and, on account of the trees and tree stumps that remain in them, they soon revert to woodland (Pl. 4, phot. 4).

There are fewer houses near the bottom of the slope and the tree growth is taller and denser. Large specimens of *Albizzia coriaria* up to 15 m. in height and 20 m. in spread, are most noticeable but there are well-grown trees of other species—*Albizzia zygia*, *Vitex fischeri*, *Combretum gueinzii* and *C. binderianum*. Just above the edge of the valley grassland there is a belt where trees and shrubs grow more densely, forming patches of thicket around termite mounds; other species are represented in such groups—the spreading *Acacia sieberiana* and the succulent *Euphorbia calycina* among the trees, and *Harrisonia abyssinica* and *Rhus natalensis* among the shrubs.

D. *Valley grassland*

The bottom of the valley, which is nearly flat, is about 200 m. wide and is covered mostly with grasses growing to a height of about 1·5–2 m. The character of the grassland is typical of that found in many similar situations in Uganda—it is composed of large tussocks of grass, spaced about 0·5–1 m. apart and raised about 15–20 cm. above the general ground level; the soil is a stiff grey clay and the uneven surface is due to treading by cattle when the ground is wet.

Two grass species are abundant in this valley grassland—in some patches *Setaria sphacelata* is locally dominant; in others *Hyparrhenia filipendula* is dominant. There are occasional tufts of *Loudetia arundinacea*, and the smaller *L. kagerensis* is common, but is not very noticeable among the taller grasses. In the low wet centre of the valley, the grassland is open and free from woody elements, but towards the sides of the valley there are some small trees of *Bauhinia thonningii*, up to 5 m. in height. Isolated specimens of larger trees—*Acacia sieberiana* and *Albizzia coriaria*—grow at the edge of the grassland, where it merges into the woodland on the slope of the hill.

The upper side of the grassland is also broken by scattered large groups of trees and

shrubs on and around low wide termite mounds; some of the groups are 15 m. across. The species growing on these mounds are mostly those which are growing in the woodlands above—*Euphorbia calycina, Albizzia coriaria, Combretum binderianum, Grewia mollis, Harrisonia abyssinica, Acacia holstii, Rhus natalensis* and *Zizyphus mauritiana*—the last species is mainly confined to the termite mound groups in the valley and is little represented in the woodland on the hill. On the ground in the centre of the groups of trees and shrubs, *Sansevieria* sp. is growing: the shade-loving grass, *Setaria chevalieri*, grows nearer the outside and, on the edge, *Panicum maximum* is a common grass. The general appearance of the woody groups on the termite mounds is of plants adapted to dry conditions—*Euphorbia calycina* is a succulent tree and *Zizyphus mauritiana* is a species common in the driest regions of Uganda.

Kakinze soils

No.	Zone	Situation	Character	pH	P	K	Ca
1	B	Banana garden near hilltop	Dark brown sandy loam	6·5	1	2	3
2	C	Cotton plot, cleared from woodland	Brown sandy loam	5·0	2	3	Trace
3	C	Banana garden close to sample 2	Brown sandy loam	7·5	1	4	4
4	D	Valley grassland	Grey clay loam	5·0	2	Trace	1
5	D	Termite mound in valley grassland	Grey clay loam	7·0	2	4	3

Three samples, numbers 1, 3 and 5, were approximately neutral and were rich in bases: two of these were from banana gardens near houses and one was from a termite mound—all three of them were from situations where biological activity would lead to a concentration of plant nutrients. There is little doubt that there is a concentration of nutrients near the houses—a comparison between samples 2 and 3 is especially illuminating, for these samples were taken close together, on the same contour of the hill; the cotton plot, recently cleared from natural woodland, had much poorer soil than that of the banana garden which had been cultivated for many years.

Discussion on Kakinze

This hill was chosen because it lies near the northern edge of the elephant grass zone: south of Kakinze, there are wide stretches of elephant grass and a dense population; north of Kakinze the population is sparse and much of the countryside is uncultivated—the hills are covered with woodland and the valleys are covered with grassland. In places more removed from human settlement, not only is there a much smaller proportion of land under cultivation, but also the effect of grazing is less evident—there is a taller growth of grass on the hills and the soil of the valley is less pocked and puddled by the treading of stock. It is interesting to note that cultivation has induced a type of vegetation which is more lush than that which was growing wild. This difference is especially noticeable in the dry season, when the grasses are parched and brown, and many of the woodland trees are leafless. Yet the banana gardens retain their vivid green, and the trees growing in them—the *Chlorophora excelsa* and the *Ficus* spp.—retain their dark canopies for most of the time.

If the banana gardens were abandoned, it is probable that they would soon be colonized by elephant grass, such as grows in thickets to the south of Kakinze, even on land which appears to have been under woodland and not under close evergreen forest. Kakinze is

outside the forest area; the total amount of rainfall is probably as great as the total amount of Kawanda, but it is less well distributed and, as the day temperature is higher, the rate of evaporation is greater.

The usual effect of human interference with tropical vegetation is to produce more xerophyllous types: closed forests are cut down to make cultivation and, when the land is exhausted, it reverts to grassland, such as would grow in drier conditions. Yet at Kakinze the process seems to be reversed: bananas and *Chlorophora* trees, plants typical of wet zones, are grown on the hilltop, while the wild vegetation in the valley comprises species such as *Euphorbia calycina* and *Zizyphus mauritiana*, which are typical of the driest districts of Uganda. One possible explanation of this anomaly may be the fact that the planting and maintenance of a banana garden near a house may lead to an increase of plant nutrients in the soil; not only is there an addition of nutrients from the refuse put on the surface of the soil but, as the banana is a very deep-rooted plant, it may bring up nutrients and water from the lower layers of soil and subsoil.

Much of the land to the north of Kakinze is not cultivated and smaller game animals are not uncommon there; the wild pig does a certain amount of damage to crops and, on that account, is hunted with dogs and nets.

Seyajongo

The hillside at Seyajongo is the most northerly of those described in this paper, and is situated at about 1° 32′ N., 32° 4′ E., close to the boundary of Buganda and Bunyoro.

As is typical of the country around Lake Kyoga, the slopes are much more gentle than those around Lake Victoria; although the stretch of hill which is described is about 4 km. long, yet the top is only about 30 m. above the river Kafu, which flows at the bottom of the hill. The climate is probably not so dry as that of the country north of Nakasongola, about 30 km. to the east, but appears to be typical of much of the north of Buganda; the average annual rainfall is probably about 1000 mm.

Six stages of the catena are clearly visible (Fig. 8):
A. Woodland on the hilltop.
B. Grassland and termite mound complex on upper slopes.
C. Grassland and termite mound complex on middle slopes.
D. Grassland on lower slopes.
E. Valley grassland.
F. River Kafu vegetation.

A. *Woodland on the hilltop*

The level hilltop is covered with woodland of scattered, spreading trees, up to 10 m. in height, with smaller trees between them and many patches of shrubs, usually grouped around termite mounds. The woody elements cover about one-third of the ground, leaving two-thirds to a cover of grass, which grows lushly to a height of 2 m. (Pl. 5, phot. 5).

Albizzia coriaria is the most common tree, forming spreading specimens up to 10 m. high; *Acacia sieberiana* is common and so is *Lannea barteri*, but they do not grow so large as the *Albizzia*. Other medium-sized trees are frequent—*Ficus gnaphalocarpa*, *F. natalensis* and *Vitex fischeri*. Smaller trees include *Combretum binderianum*, *Grewia mollis*, *Zizyphus mauritiana* and *Bauhinia thonningii*—all of them species which are common in the drier woodlands of Buganda. Small trees—*Acacia holstii* and *Dichro-*

stachys glomerata—growing in groups are regarded as indicators that there have been settlements here in the past, and so is the *Chlorophora excelsa*, of which there are one or two specimens (Thomas, 1944).

The smaller trees are not evenly distributed over the ground, but are most abundant around the termite mounds; *Euphorbia calycina* is frequent in the groups around the mounds, but is not found at a distance from them. *Harrisonia abyssinica*, a scandent shrub, is a very common constituent of the dense mass of woody plants in the anthill colonies; and *Landolphia florida* and *Clematis incisodentata* are common climbers in these groups.

Hyparrhenia filipendula is the dominant species in the strips of grassland between the colonies of shrubs, while *Imperata cylindrica* and *Setaria sphacelata* are common. On the outside of the colonies of shrubs and on the roadside, situations where the soil is more
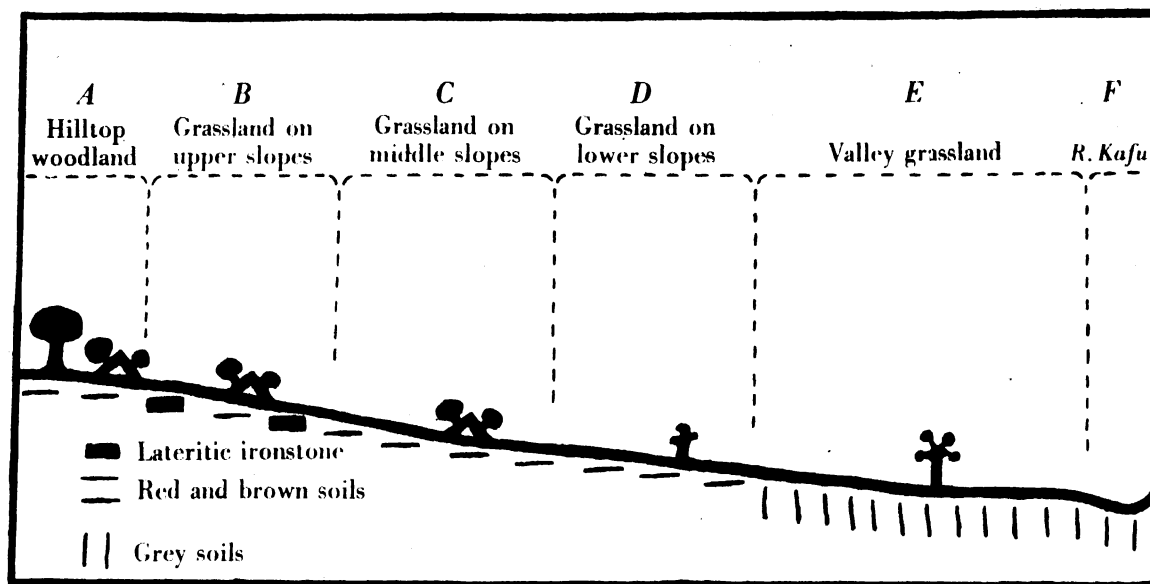
Fig. 8. Diagram of catena at Seyajongo.

fertile than the average of the grassland, *Panicum maximum*, *Brachiaria brizantha* and *Chloris gayana* are common grasses.

At the present time there is no settlement in this area but at a little distance to the east there is a considerable population. The main food crop is cassava: small patches of bananas and sweet potatoes are grown. Annual food crops are important—maize, beans, simsim and finger millet (*Eleusine coracana*); large plots of ground are roughly cleared from woodland, the trees coppiced and cotton planted as an export crop.

There are no cattle in this area now—they all died about three years ago from trypanosomiasis when tsetse fly (*Glossina pallidipes*) spread into it. Sheep and goats still flourish and have an abundance of grazing. Because of the small population and of the abundance of grass, wild animals are numerous. Wild pig and small duiker do much damage to crops; at times buffalo also come into the farms and cause much damage. Elephants, which are very troublesome in cultivations to the south and west, do not visit this neighbourhood often.

Phot. 5. Seyajongo catena. Hilltop woodland (zone A).

Phot. 6. Seyajongo catena. Valley grassland in the dry season (zone E):
scattered *Borassus flabellifer* and *Imperata cylindrica* in flower.

B. *Grassland and termite mound complex on upper slopes*

There are fewer trees on the slopes of the hill than on the level top, and the character of the vegetation is better described as a grassland: for the grasses are the most important members of the community and the woody elements are confined to the frequent groups around termite mounds. *Hyparrhenia filipendula* is the dominant grass, and *H. dissoluta* is common. Both species grow in small tufts, with much bare ground between them, but their inflorescences form a fairly even cover at a height of nearly 2 m. A few herbs grow between the grasses. In two places, at about 100 m. and 200 m. below the crest of the hill, there are outcrops of ironstone, whose upper surface is parallel to the slope of the ground; in some places the ironstone is bare; in others, there is a thin cover of soil in which the dwarf grasses, *Sporobolus festivus* and *Microchloa kunthii*, grow to a height of about 25 cm.

Euphorbia calycina is the most characteristic species of the woody groups around the termite mounds and specimens up to 8 m. high are common. Other common tree species in these groups are *Vitex fischeri*, *Combretum gueinzii*, *Zizyphus mauritiana*, *Grewia mollis* and *Acacia holstii*, while *Vitex cuneata* and *Strychnos innocua* are less frequent. The stretches of open grassland form a violent contrast to these dense masses of trees and shrubs around termite mounds, whose growth is almost impenetrable when the prickly scandent shrubs, *Acacia pennata* and *Harrisonia abyssinica*, grow among and over them.

C. *Grassland and termite mound complex on middle slopes*

The second zone is on the steeper slopes near the top of the hill, and merges into this zone, which covers the greater part of the slopes of the hill. It is of the same type as zone B, but differs in some details:

(*a*) There are fewer anthill colonies and most of the zone is made up of grassland in which *Hyparrhenia dissoluta*, growing to a height of about 2 m., is dominant. *Hyparrhenia filipendula* is common, and so is *Setaria sphacelata*. Many patches of cotton have been grown in this zone in recent years and the land which has been abandoned is covered with a mass of *Imperata cylindrica*, a species which is present, but only in small amounts, in the grassland which has not been disturbed for some time. There are clumps of *Hyparrhenia rufa*, growing to a height of nearly 3 m., near some of the anthills; *Panicum maximum* and *Brachiaria brizantha* are common near anthills and beside the road.

(*b*) Not only are the colonies of trees and shrubs around termite mounds less common, but also they are more open in growth than those in the zone above. *Albizzia zygia* is very common on the woody groups. *Ficus gnaphalocarpa*, *Erythrina tomentosa*, *Steganotaenia araliacea* and *Grewia mollis* are common trees; and *Harrisonia abyssinica* is the most common shrub. Specimens of *Borassus flabellifer* are scattered in the grassland away from the termite mounds.

D. *Grassland on lower slopes*

There are fewer termite mounds on the lower slopes of the hill and the vegetation consists for the most part of open stretches of grassland, in which *Hyparrhenia dissoluta*, mixed with *H. filipendula*, grows to a height of 2 m.: there is also some *Imperata cylindrica* in most parts of the grassland.

There is a small group of huts at the base of the hill, on a slight rise in the ground.

Around them are some small banana gardens and patches of cassava, maize and cotton. Near these houses are stretches of land, now under a thick cover of *Imperata*, on which cotton has been grown in past years.

Borassus palms are thinly scattered in this zone. *Ficus gnaphalocarpa*, *Euphorbia calycina* and, less frequently, *Acacia sieberiana* grow close to the occasional termite mounds. The tops of the mounds are bare but, near their bases, the mounds are colonized by grasses such as *Chloris gayana* and *Setaria incrassata*. It is interesting to note the latter species on the termite mounds, for it is a species typical of 'black cotton soil', the dark calcareous clay which is found in valley bottoms in the drier parts of northern Uganda (Thomas, 1944). *Setaria incrassata* is tolerant of waterlogged soil for considerable spells; yet it grows on the mounds, while the grasses which grow on the soil below are less tolerant of waterlogging. The reason for this anomalous distribution lies in the difference in soil composition—that of the mounds in a calcareous clay, while the soil around is poorer in lime and in clay content. A pit dug to a depth of 1 m. showed a profile of grey sandy clay on the surface slowly merging into a light brown sandy clay at a depth of 1 m.

E. *Valley grassland*

There is a wide stretch of grassland at the base of the hill, sloping very gradually down to the river Kafu, over 1 km. away: some of the land near the river is under water in very wet seasons.

The grassland is very mixed, especially near the ferry over the river; there is usually a sparse thin cover of grasses growing to a height of about 1 m. above the grey sandy soil. In some places *Setaria incrassata* is dominant, in some places *Hyparrhenia filipendula*; and in some places *H. rufa* forms dark patches, growing to a height up to 2 m., conspicuous among the other grasses. *Chloris gayana*, *Themeda triandra*, *Heteropogon contortus* (on knolls) and *Bothriochloa insculpta* are other grasses found in this zone. *Imperata cylindrica* is abundant.

There are very few trees: *Borassus flabellifer* is thinly scattered over the ground; *Ficus gnaphalocarpa* occurs on some termite mounds; *Acacia seyal* grows in some of the depressions. But the general effect is one of almost level, open, grassland (Pl. 5, phot. 6).

The soil is grey, a mixture of clay and sand; in some of the higher parts the surface is sandy, but in the hollows it is of clay, very tenacious when wet and cracking deeply when it is dry.

F. *River Kafu vegetation*

Close to the banks of the river, there are patches of *Hyparrhenia rufa*: the banks themselves are covered with *Phragmites mauritiana*, growing to a height of 3 m.; *Sesbania aegyptiaca*, a soft-wooded tree, is frequent. In some places, sheltered from the main force of the current, *Cyperus papyrus* grows in dense patches to a height of 3 m. above the usual water level.

On the edge of the water the grass, *Sacciolepis africana*, and *Jussiaea* sp. grow, rooted in the mud and floating in the water. In the centre of the stream, a mauve *Nymphaea* sp. is common.

The Seyajongo soils as a whole are greyer and are less acid than those from the wetter parts of Buganda. But, like those from other catenas, they illustrate the concentration of bases in and around termite mounds.

Seyajongo soils

No.	Zone	Situation	Character	pH	P	K	Ca
1	A	Grassland, *H. filipendula* dominant	Pale brown loam	6·0	2	1	1
2	A	Termite mound colony	Pale brown loam	7·0	1	3	3
3	D	Patch of old cultivation, *Imperata* dominant	Grey sand	6·0	3	3	2
4	D	Termite mound, *Setaria incrassata* dominant	Grey clay	7·5	2	3	3
5	E	Mixed grassland in valley	Grey sandy clay	6·5	2	1	2

Discussion on Seyajongo

This hillside is in drier and less populated country than the other ones described above: although there are signs of recent interference with the vegetation at Seyajongo, yet the cultivated area is in much smaller proportion to the uncultivated than in the other localities. And, on account of the influx of tsetse fly, there is now no grazing by cattle: in consequence the grass can grow unrestricted and the ground beneath is less trodden.

The Seyajongo catena exhibits well a feature of the distribution of vegetation in the drier parts of Africa—that there are more trees and shrubs on the ridges than in the hollows. Michelmore (1939) has described this phenomenon and has suggested that trees do not grow in the valleys because they are intolerant of waterlogging; yet at Seyajongo, trees are scarce even on the lower slopes of the hill, in places where there is never any waterlogging.

It is interesting to note that in all zones of the catena there is a concentration of woody elements on and around the termite mounds but, while many trees are growing in grassland on the hilltop away from the mounds, yet on the lower slopes of the hill and in the valley the trees, with the exception of the *Borassus* palms and *Acacia seyal*, are mainly confined to the termite mounds. *Acacia seyal* is abundant in parts of the Karamoja district of Uganda and it has been postulated that the frequence of the tree may be correlated with the overgrazing of valley grassland (Thomas, 1944). It is probable that the same explanation may be given of its occurrence at Seyajongo.

Yet it is difficult to explain the distribution of the *Borassus* palms; they are mostly mature, about 10 m. high, and there is not very much regeneration. This palm occurs in scattered localities of Uganda and is locally abundant in those places, but it is difficult to ascertain any climatic or edaphic factors which influence the distribution. It has been suggested that the seeds are carried by elephants, which are fond of the fruits; and, as the fruits are also used as food by some tribes, it is probable that human influence is also involved in the distribution.

REFERENCES

Martin, W. S. (1944). Grass covers in their relation to soil structure. *Emp. J. Exp. Agric.* **12**, 21–32.

Martin, W. S. & Griffith, G. (1940). Uganda soils. *Agriculture in Uganda*, p. 64.

Michelmore, A. P. G. (1939). Observations on tropical African grasslands. *J. Ecol.* **27**, 282–312.

Milne, G. G. (1935). Some suggested units of classification and mapping, particularly for East African soils. *Soil Res.* **4**, 183–95.

Milne, G. G. (1936). *Report on a Soil Reconnaissance Journey in Tanganyika Territory.*

Thomas, A. S. (1941). The vegetation of the Sese Islands, Uganda. *J. Ecol.* **29**, 330–53.

Thomas, A. S. (1942). A note on the distribution of *Chlorophora excelsa* in Uganda. *Emp. For. J.* **21**, 1.

Thomas, A. S. (1944). The vegetation of the Karamoja District, Uganda. *J. Ecol.* **31**, 149–77.

THE REGENERATION OF DOUGLAS FIR, *PSEUDOTSUGA TAXIFOLIA* BRITT., IN THE NEW FOREST

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(*With two Figures in the Text*)

INTRODUCTION

Douglas fir, *Pseudotsuga taxifolia* Britton, was introduced to this country in 1827, but was used only as an ornamental tree for many years, so that there are few old stands of it in Britain. In the New Forest it was planted to a limited extent in some of the Inclosures made following the Act of 1851. Usually it was only used in marginal lines along rides, etc., but in Boldrewood Grounds a mixture of equal amounts of *Pseudotsuga*, *Cedrus deodara* Lawson and *Pinus sylvestris* L. was planted. *Pseudotsuga* has far outgrown its companions, which have now almost disappeared except at ride sides. In all these early plantings the Douglas were given ample space and grew quickly, so that they are now of impressive size. During the past twenty years regeneration has been appearing near all of them, and attempts are being made on an experimental scale to regenerate a small part of the Boldrewood stand. Natural regeneration of Douglas fir has also been observed in other parts of the country, e.g. Devon, Northumberland and Scotland, and there is every indication that it may naturalize itself fully in this country, and regenerate as freely as Scots pine. The condition and progress of its regeneration in the New Forest has been studied with the help of members of the staff and students of the Imperial Forestry Institute during 1941–3 in Busketts Lawn Inclosure, which was made in 1864 and planted shortly after. Some additional information has been gathered from Shave Green, another Inclosure of the same period, where ride-side lines of Douglas make a splendid avenue through crops of oak, Scots pine and larch.

SITE CONDITIONS

Busketts Lawn Inclosure lies in the shallow valley of Bartley Water about 2 miles east of Lyndhurst. The portion with which we are concerned lies on an ancient flood plain of alluvial silts, loams and gravels through which the present stream runs at the bottom of a meandering channel incised some 4–5 ft. into the plain. The ground near the stream banks is slightly higher than that farther away and is thus better drained. There is therefore a well-marked zonation of soil types on either side the stream, due fundamentally to drainage conditions, but accentuated by variation in soil texture. Fig. 1 illustrates this zonation diagrammatically. Three major soil regions may be distinguished:

I. Remote from the stream are gleyed podsols with 20–25 cm. of leached sandy loam or heavy sand overlying strongly gleyed clays. There is usually 5–8 cm. of raw humus—probably remaining from the former vegetation—with a further 5–8 cm. of pine litter and humus.

II. As the stream is approached the degradation decreases, and the surface soil usually becomes heavier. There is thus an irregular belt of heavy loams of Brown Forest Soil type, where as a result of heaviness of soil gleying may approach to within 8 cm. of the surface. The humus is typical mull.

III. Between zone II and the stream deep well-drained loams predominate. They are scarcely gleyed, often silty, and are brown forest soils. The humus is mull, although on account of the crop there is a continuous litter 1–3 cm. thick of Douglas fir needles.

The natural zonation of vegetation associated with the various soils is obscured by differences in the planted crop. Prior to 1940 the greater part of the area bore pure Scots pine, but a belt some 90–120 m. (300–400 ft.) wide along the course of the stream bore pure Douglas fir, while on either side of it was a narrow region of variable extent where oak (*Quercus robur* L.) was mixed with the pine, or even locally replaced it. In many Inclosures of this period a mixture of oak with pine for nurse was planted, as in some other parts of Busketts Lawn and adjacent inclosures, and in Shave Green, and according to the relative vigour of the two species on the soil in question sometimes one and sometimes the other has been suppressed or even exterminated. It is not certain whether oak was planted or is spontaneous in the present area, but most of the available evidence points to its being spontaneous. In either case its presence demonstrates the
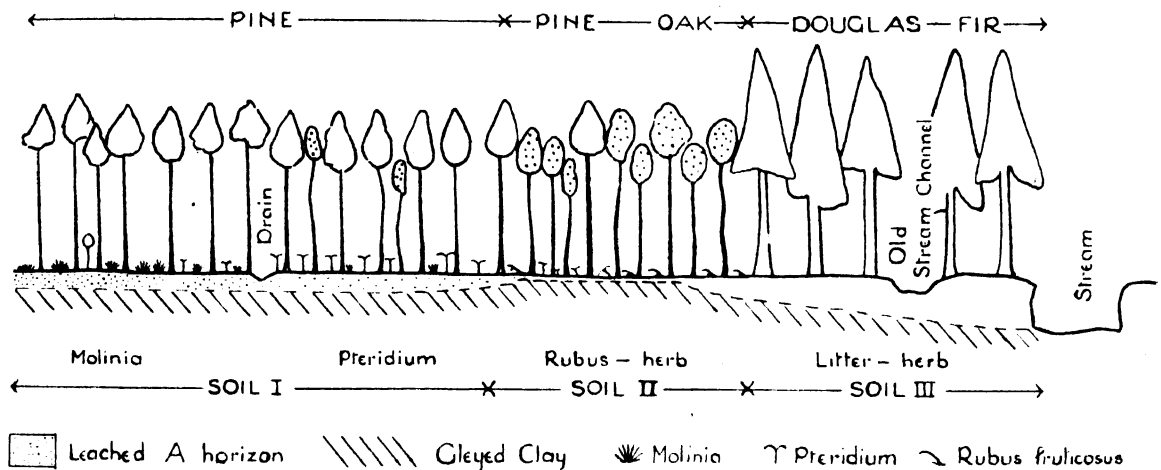
Fig. 1. Diagram showing zonation of soil, ground vegetation and crop in
Busketts Lawn Inclosure.

effect of the more basic soils towards the valley centre, since if planted it would certainly have been mixed with the pine over the whole block.

The survey of the forest by Richardson, King, Driver & Abraham in 1787 shows that there was then a belt of woodland along the sides of the stream on approximately the same area as the Douglas fir, while on either side, where the pine was subsequently planted, were treeless grazed 'Lawns'. There would thus have been abundant oak seed in the area near the stream. In a general way therefore, the pine region corresponds to soil zone I, the oak-pine region to soil zone II, and the Douglas fir region to soil zone III, though of course the coincidence of soil and crop boundaries is not close, especially for the Douglas fir crop.

In 1941, when 77 years old, the pine was 25–27 m. (80–87 ft.) tall and there were about 520 stems per ha. (210 per acre). Although there were frequent stunted oak 0·5–2·0 m. tall beneath, and also occasional chestnut (*Castanea sativa* Mill.), holly (*Ilex aquifolium* L.) and *Betula* spp. beneath it, there was no true understorey. There were two well-marked and often sharply defined types of ground vegetation, with *Molinia coerulea* and *Pteridium*

aquilinum as the respective dominants. The *Pteridium* type was much the more restricted, and usually on the better drained, less degraded soils nearer the stream. The following is a typical example of the *Molinia* type:

Canopy, pure Pinus sylvestris

Molinia coerulea	c.d. 40% cover	Polytrichum formosum Hedw.	o.
Rubus fruticosus agg.	c.d.	Thuidium tamariscinum B. & S.	v.a.
Ilex aquifolium, 1 ft. tall	f.	Hypnum schreberi Willd.	v.a.
Hedera helix	o.	Brachythecium purum Dixon	v.a.
Calluna vulgaris	r.	Hylocomium splendens B. & S.	o.
Vaccinium myrtillus, clans	v.l.	Lophoclea cuspidata Limpr.	o.
Agrostis alba	r.		
Luzula congesta	r.		
Galium saxatile	r.		
Potentilla erecta	r.		
Teucrium scorodonia	r.		

Bryophyte cover 40%
Conifer litter cover 20%
Phanerogam cover 40%

The following is an example of the *Pteridium* ground vegetation:

Canopy, pine with occasional oak

Pteridium aquilinum	d. 60% cover	Deschampsia flexuosa	l.a.
Rubus fruticosus	v.a. 30% cover	Carex pilulifera	o.
Molinia coerulea	v.a. 30% cover	Ilex aquifolium	o.
Hedera helix	l.a.		

Bryophytes; species as in *Molinia* type, cover 20%
Conifer litter cover 20%
Phanerogam cover 60%

In more extreme examples *Pteridium* is tall and dense and has little else but *Rubus fruticosus* growing with it. Whether there is a well-marked *Pteridium* zone or not, transect data show a gradual increase of *Pteridium* in passing from the valley sides towards the centre, and the *Pteridium* zone is transitional in several respects between the *Molinia* zone and the oak-pine region.

In the oak-pine region the oak is of the same age as the pine, and there are frequent patches of pure oak. *Pteridium* is not abundant, and often absent. *Rubus fruticosus* is often more abundant and luxuriant than on the preceding soils, and while *Molinia* remains abundant, in lighter places there is also much *Agrostis tenuis*, *A. alba*, and locally *Holcus mollis*, *Deschampsia flexuosa*, and *Brachypodium silvaticum*. There are frequent carpets of *Oxalis acetosella*, and small amounts of *Viola riviniana*, *Lysimachia nemorum*, *Euphorbia amygdaloides* and similar herbs. *Hylocomium loreum* B. & S. and *Eurhynchium striatum* B. & S. are abundant and characteristic mosses. The whole region is variable, and it is difficult to select a typical sample for listing, as has been done with the *Molinia* and *Pteridium* types.

The Douglas fir was 36–38 m. (120–127 ft.) high in 1941, and, despite its wide spacing, so dense that there is now a continuous carpet of needles beneath it, with no ground vegetation except in slight gaps where there are carpets of *Oxalis*, with herbs such as *Viola riviniana*, *Lysimachia nemorum* and *Sanicula europea*. Ash (*Fraxinus excelsior* L.) seedlings are abundant in some of the larger gaps. Despite the paucity of vegetation,

the floristic richness of this region bears testimony to the more basic soil. The Douglas fir belt as a whole, including the stream banks, yields species such as *Circaea lutetiana*, *Carex remota*, *Primula acaulis*, *Mercurialis perennis*, *Festuca gigantea*, *Sorbus torminalis* (seedlings), *Geranium robertianum* and *Deschampsia caespitosa*, several of which are rare species in New Forest woods.

RECENT HISTORY OF AREA AND PROGRESS OF WORK

In the winter of 1940-1 some blocks of pine were felled for regeneration, 20-30 trees per acre being left to provide seed for restocking, and similar treatment of other blocks continued through the summer of 1941 up to the spring of 1942. During the autumn and winter of 1941 the Douglas fir was heavily thinned, while throughout 1942 and 1943 there was felling of oak. Studies have been made in four blocks bounded by rides, which for convenience will be referred to by letters, and which represent the following three conditions:

Block A.   Pine regeneration fellings made in summer 1941-spring 1942.
Blocks B, C. Pine regeneration fellings made in winter 1940-1.
Block D.   Pine lightly thinned, but no regeneration fellings yet made (autumn 1943).

When work began in 1941, Douglas fir regeneration was most abundant in block D, being present on all soils in the oak-pine and pine regions, sometimes scattered singly, but more often in groups, with trees up to 305 cm. (10 ft.) high. Four belt transects (about a 1 % sample) were made across the valley, the number, height and age (determined by counts of branch whorls) of all young *Pseudotsuga* present within adjacent 6 × 6 ft. (183 cm. square) quadrats being recorded. Reassessments have been made on three out of the four transects in 1942 and 1943, but since the object has been to study the entry of fresh seedlings rather than the amount of older regeneration, 6 ft. quadrats were replaced by quadrats 2 ft. (61 cm.) square spaced at 6 ft. intervals. In these two latter years however attention has been devoted mainly to blocks A-C, which had then been felled. These were also studied by 2 ft. square quadrats spaced at 6 ft. intervals on transects across the valley. The number and age of tree seedlings present was recorded, and also percentage cover by litter, *Molinia*, *Rubus fruticosus*, *Pteridium*, moss, grasses other than *Molinia*, and phanerogams other than these. The samples in 1942 and 1943 amounted to 0·05-0·1 % of the total area.

SEED PRODUCTION BY DOUGLAS FIR

Entry of new seedlings into the Busketts Lawn crop is certainly periodic, and this appears to be due to erratic seed production. In 1941 only a single first-year seedling was found, and second-year seedlings were equally rare; third-year seedlings (germinated 1939) were the youngest present in any appreciable number. In 1942 first-year seedlings were abundant throughout the New Forest; in 1943 they were very much scarcer, though more abundant than in 1941. The first and second lines of Table 1 compare the figures for 1942 and 1943.

Table 2 shows the age classes recorded in the 1941 transects. There is, of course, liability to underestimation in determining ages from branch whorls, and it is practically certain that the seven plants recorded as 2-year-olds were in fact small 3-year-olds; I myself was

Table 1. *Numbers of Douglas fir seedlings in Busketts Lawn Inclosure, 1942 and 1943*

| | Block A | | | | | | Blocks B, C | | | | | | Blocks A–C | | |
| | Molinia | | | Pteridium | | | Molinia | | | Pteridium | | | All vegetation types | | |
	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
(1) 1st yr. seedlings, 1942	169	8·8	0·106	75	18·7	0·20	114	0	0	97	9·3	0·082	455	8·35	0·091
(2) 1st yr. seedlings, 1943	80	1·25	0·025	58	5·2	0·069	95	0	0	73	0	0	306	1·31	0·020
(3) Seedlings of all ages, 1942	169	8·8	0·106	75	18·7	0·20	114	0	0	97	9·3	0·082	455	8·35	0·091
(4) 2nd yr. and older seedlings, 1943	80	3·75	0·037	58	19·0	0·224	95	3·12*†	0·042*	73	1·4*	0·014*	306	6·2	0·069

Block D

| | Pine crop | | | Pine-oak crop | | | Douglas crop | | | All crops | | |
	a	b	c	a	b	c	a	b	c	a	b	c
(1) 1st yr. seedlings, 1942	64	4·7	0·047	48	4·2	0·083	79	41	0·785	191	19·9	0·371
(2) 1st yr. seedlings, 1943	67	0	0	40	5·0	0·050	51	23·5	0·432	158	8·9	0·171
(3) Seedlings of all ages, 1942	64	7·8	0·079	48	4·2	0·083	79	41	0·785	191	20·9	0·381
(4) 2nd yr. and older seedlings, 1943	67	7·5	0·090	40	12·5‡	0·225	51	19·6*	0·373*	158	12·7*	0·215*

* Probability of difference from 1942 figures arising by chance less than 0·05; column b tested by χ^2, column c by assuming that the variance equals the mean (Poisson distribution).

† Three quadrats in a single transect.

‡ Five quadrats in a single transect.

Column a = total number of quadrats.

b = percentage of the above number with Douglas fir seedlings.

c = mean number of seedlings per quadrat.

unable to find a single certain example of a second-year seedling. The figures suggest maxima in the 3-year (1939), the 7-year (1935) and the 10-year (1932) classes, but the numbers in the intervening classes are so large as to suggest that there has been some establishment in some of these years. It is, for example, hardly likely that all the eleven plants recorded as 4 years old were in fact 7 years old.

Table 2. *Age classes of Douglas fir seedlings in Busketts Lawn Inclosure*

(a) In the transects

Age class	Germinated in	Transect no. 1	2	3*	4	1–4
1†	1941	.	?1	.	?2	?3
2†	1940	?2	?2	?2	?1	?7
3	1939	1	11	6	.	18
4	1938	.	7	2	2	11
5	1937	2	8	4	3	17
6	1936	5	6	4	3	18
7	1935	3	19	3	3	28
8	1934	10	8	3	2	23
9	1933	7	7	1	1	16
10	1932	15	4	.	.	19
11	1931	8	1	.	.	9
12	1930	3	.	.	.	3
13	1929	2	.	.	.	2
14	1928	.	1	.	1	2
17	1925	.	.	.	1	1
Range of ages (years)		11	12	7	15	17
No. of seedlings		58	75	25	19	.

* Five additional seedlings in transect 3, ages unspecified, but greater than 10.
† All records of 1 and 2 yr. old seedlings very doubtful.

(b) In single groups of regeneration

Age class	Germinated in	a	b	c	d	e	f	g	h	i	j	k	l	m	n
1	1941	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2	1940	.	.	.	.	.	.	.	.	?1	.	.	.	.	?1
3	1939	.	.	.	.	.	.	.	1	.	.	1	3	1	4
4	1938	1	2	1	.	.	.	.	1	.	1	.	.	1	2
5	1937	.	2	.	1	1	1	.	1	2	1	1	.	.	3
6	1936	1	3	1	.	.	2	1	.	.	.	2	.	1	.
7	1935	.	7	1	.	4	.	1	.	1	2	.	.	.	3
8	1934	1	2	1	2	3	3	3	.	.	.	1	1	1	1
9	1933	1	5	1	1	1	2	1	1	.	1	.	.	.	.
10	1932	.	2	5	2	1	6	.	.	.	.	.	.	.	.
11	1931	.	.	3	2	.	3	.	.	.	.	.	.	.	.
12	1930	.	.	1	1	.	.	.	.	.	.	.	.	.	.
13	1929	.	.	1	.	.	.	.	.	.	.	.	.	.	.
14	1928	2	1	.	.	.	.	.	.	.	.	.	.	.	.
Range of ages (years)		10	10	9	7	5	6	3	6	5 or 4	5	5	5	5	6 or 5
No. of seedlings		6	24	15	9	10	17	6	4	4	5	5	4	4	14

The Busketts Lawn Douglas are probably only just attaining full bearing capacity. In 1941 only a quarter of the trees had any fallen cones beneath them, and cones were present on scarcely any of the trees that were felled that autumn. In 1942 and 1943, when many of the adjacent crops had been felled and the Douglas itself thinned, it was possible to get further information on cone production by examining the crowns with binoculars, and trees in the avenue in Shave Green Inclosure were examined in the same way. The results of these assessments are given in Table 3.

These figures confirm the fact that in Busketts Lawn, where it must be remembered a number of the smaller trees had already been felled, only a small proportion are yet coning. By the ride side in Shave Green, however, coning is much better.

Table 3. *Numbers of Douglas fir bearing cones of the current year*

	1942 Number of trees bearing				1943 Number of trees bearing			
	Many cones	Few cones	No cones	No cones of any age	Many cones	Few cones	No cones	No cones of any age
Busketts Lawn:								
No.	0	3	72	40	0	12	28	*
%	0	4	96	53	0	30	70	*
Shave Green:								
No.	1	10†	79	10	2	3	75	13
%	1	11	88	11	2½	4	94	16

* Not recorded.
† Only a single cone seen on each of four of these.
All figures refer to current year's cones, except for the fourth and eighth columns.

THE DISTRIBUTION OF ESTABLISHED REGENERATION

The established regeneration of block D is present throughout the oak-pine and pine regions, but is very irregular in distribution, much of it being localized in groups which may be up to 18–27 m. (20–30 yd.) across. This irregularity is demonstrated by the fact that for the pine and pine-oak regions the average density was 0·102 seedlings per sq.m. (0·443 per quadrat), while the maximum density for an area of 20 sq.yd. (16·7 sq.m.) was 1·02 per sq.m., and 40% of the quadrats containing seedlings were in groups of three or more consecutive quadrats. The young trees are not distributed at random, and the frequencies of quadrats with 0, 1, 2, ..., etc., seedlings do not fall on a Poisson distribution. The mean number of seedlings per quadrat is 0·443, the calculated variance 1·23, and the relative variance (cf. Clapham, 1936) 2·8. The causes for this aggregation of young plants might either be that conditions were unsuitable for germination and early growth of the seedling, or for its later growth. Groups of regeneration are present through the whole of the pine and pine-oak regions, but despite the fact that the latter is much nearer the source of seed it is much more poorly stocked. This is the explanation of the low initial values for the curve in Fig. 2, and is also shown by the following figures (for block D, 1941):

	Beneath pure Scots pine		Beneath oak and pine-oak
	On podsols	On brown forest soil	On brown forest soil
Total number of quadrats	234	85	88
No. of quadrats with Douglas fir seedlings	55	28	12
Total number of Douglas fir seedlings	97	66	15
Percentage of quadrats with Douglas fir	23·5	30·3	13·6
Mean number of Douglas fir per quadrat	0·414	0·777	0·170

Proportion of quadrats with Douglas fir seedlings beneath pine = 83/319.
Proportion of quadrats with Douglas fir seedlings beneath oak-pine = 12/88.
$\chi^2_{(1)}$ for this difference = 8·0; $P = 0·004$.

It appears to be the nature of the crop rather than that of the soil which is responsible for the poor stocking of the oak-pine region. The patches where regeneration is abundant in this region are often small and sharply limited, and invariably have thick (2·5–7·6 cm.,

1–3 in.) pine litter in contrast to areas close by where regeneration is absent, and which have very thin pine litter or pure deciduous litter. This dependance on the kind of litter has been fully confirmed by studies of the distribution of first-year seedlings in 1942.

While saplings of all ages up to about 20 years are present in block D as a whole, in any one group the range of ages is restricted. The figures in Table 2 show that while in the whole area there are 3-year, 7-year, and 10-year age maxima, transect 2 has only the 3-year and 7-year maxima, while transects 1 and 3 have only one well-marked maximum each, the 3-year and 10-year respectively. This table also gives the age-class composition of the principal groups of regeneration crossed by the transects (gr ups of five or more seedlings in ten consecutive yards of transect). Some of the groups (e.g. *c*, *g*, *e*) have only one maximum each, and when they have more (e.g. groups *b*, *n*) only one year separates them. The figures also suggest that the older the oldest plants in a group, (i) the
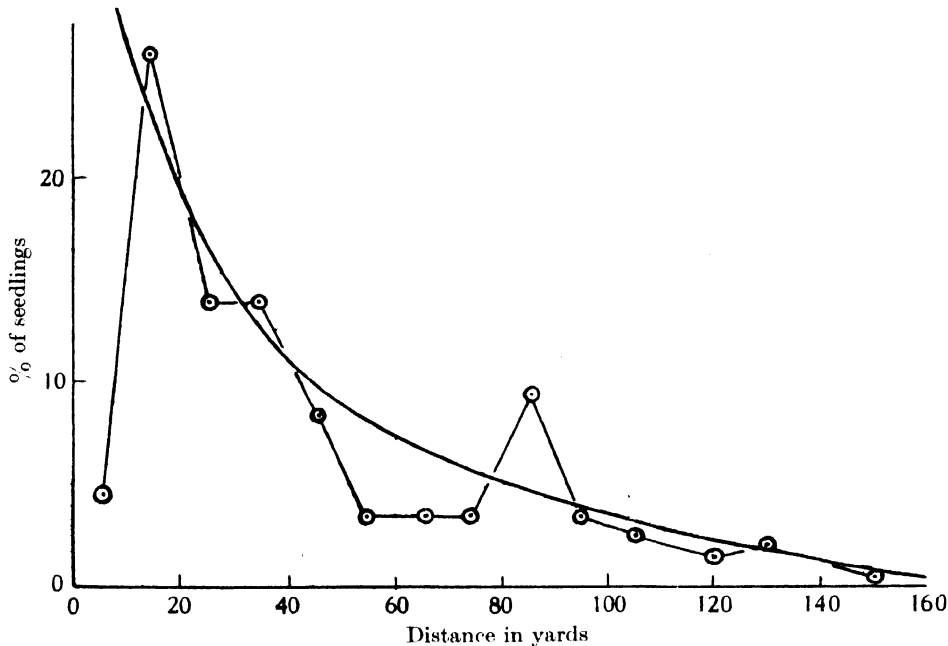
Fig. 2. Relation between distance northwards from seed-trees and number of young Douglas fir. Block D, Busketts Lawn Inclosure, 1941.

less recently has been the latest recruitment of new seedlings, and (ii) the earlier was the principal colonization. This evidence all suggests that in any one area the ground does not ordinarily remain in a receptive condition suitable for free establishment for more than a period of about 5–7 years.

CONDITIONS FOR ESTABLISHMENT OF FIRST-YEAR SEEDLINGS

In 1942 the abundance of first-year seedlings together with the variety of conditions provided by recent fellings gave an excellent opportunity for obtaining information on the kind of ground cover suitable for early growth.

(a) Entry in the Douglas fir region

First-year seedlings are by far the most abundant in the Douglas fir region, beneath the thinned crop, as the figures in Table 1 show. It appeared that undisturbed thick litter was relatively poorly stocked, but slight disturbance was favourable. Thus the

edges of tractor tracks, where the humus crust had been moved but not destroyed, had many seedlings, but the tracks proper with hardened and sometimes puddled soil were completely barren. Thin litter over mineral soil seemed to be very favourable, and seedlings were not infrequent on exposed mineral soil where this had not been compacted or greatly disturbed. Abundant seedlings have also been seen in mounds of sawdust. In a sample of thirty-nine regularly spaced 2 ft. (61 cm.) square quadrats in block B in 1942, only thirteen (33%) had no seedlings, while eight (20%) had 3–8 seedlings each. The thirteen blank quadrats were accounted for as follows:

5 quadrats.	Carpet of herbaceous vegetation (mainly *Oxalis acetosella*, with *Viola riviniana*, etc.)
4 „	On dragging or tractor tracks.
2 „	On piles of lop and top.
2 „	Apparently suitable for colonization; absence of seedlings presumably due to chance.

Even a thin carpet of herbaceous vegetation appeared to prevent seedling establishment almost completely.

(b) *Entry in the pine-oak region*

In a part of the pine-oak crop which had been felled for regeneration in 1941–2 seedlings were extremely local, and always confined to areas formerly beneath pine trees, where there was pine litter. Of twenty random 2 ft. (61 cm.) square quadrats none had seedlings, while of twenty quadrats located by pine stumps thirteen had seedlings. If it be assumed that in this region the chance of getting a quadrat with a seedling is 13/40, then from the binomial $(13/40 + 27/40)^{20}$ the probability of obtaining by chance a sample of twenty quadrats without seedlings would be about 0·0004. Comparison of the quadrats near the pine stumps with the remainder shows that the principal difference lies in the higher proportion of litter and the fact that this is conifer rather than deciduous. Near the stumps 100% of the quadrats contain conifer litter and its maximum cover recorded is 80%, while in the random quadrats only 20% contain conifer litter, and its maximum cover is 20%.

An assessment of young regeneration by means of 2 ft. (61 cm.) square quadrats was also made in the various crops near the avenue in Shave Green Inclosure. Out of forty quadrats containing Douglas seedlings only one was beneath a canopy containing deciduous species, while of forty-eight quadrats without seedlings fifteen were beneath a mixed pine-deciduous canopy, and thirty-three beneath pure pine ($\chi^2_{(1)}$ for this difference = 12·15; $P = 0·001$). Thus it seems quite clear that thick pine litter is favourable for regeneration, and that seedlings do not establish themselves, even in the absence of canopy, in litter which is predominantly deciduous.

(c) *Entry in the pine region, and further examination of effect of ground conditions*

Study of the distribution and ages of the older seedlings and saplings suggested that ground conditions were only locally suitable for seedling establishment, and remained suitable for a relatively short period. Areas where the younger age classes are present in the pine region always have little vegetation and much litter and thin moss of species such as *Hypnum cupressiforme* var. *ericetorum* B. & S., *Hypnum schreberi* Willd., *Dicranum scoparium* Hedw., etc. These features also characterize the areas where first-year seedlings were present in 1942.

A more precise evaluation of the effect of the nature of the ground cover on regeneration has been obtained by a statistical treatment which is outlined in the appendix. These

tests confirm the importance of a high cover by litter, but in Shave Green and in Busketts Lawn, blocks A–C, the association between regeneration and the total cover of moss + litter + bare ground is much stronger than with litter or moss alone. Phanerogamic cover in general appears to be unfavourable. The adverse effect of even a low cover of *Vaccinium myrtillus* is especially striking, since quadrats with *Vaccinium* usually have a high cover of moss and litter; the average cover of moss + litter for quadrats with 25 % or more *Vaccinium* is 50%. *Vaccinium* may perhaps prevent establishment mainly through root competition. The fact that in Shave Green *Rubus fruticosus* appears to be associated with favourable conditions is curious. The number of quadrats with *Rubus* is not large however, and its cover is small; it is greater than 10 % only in 2/13 quadrats. Possibly the association arises merely because both *Rubus* and Douglas fir seedlings are more shade-tolerant than the other field-layer species.

SUBSEQUENT PROGRESS OF REGENERATION

The difference between the figures in the third and fourth lines of Table 1 for total number of seedlings in 1942 and second year + older seedlings in 1943 gives the mortality, within the limits of sampling error. There appear to be very different mortality rates in the different regions, but it is unfortunately impossible to make a satisfactory estimate of the significance of the differences.

The greatest mortality apparently took place in the Douglas region, where despite thinning the shade was still too dense to permit of more than local establishment. In the *Pteridium* there appears to have been a heavier mortality in blocks B and C than in block A; Scots pine seedlings show a parallel behaviour. This may well be because blocks B and C were felled a year before block A, and the bracken is correspondingly denser.

The mortality in the *Pteridium* region of block A appears to have been very slight, and since the sampling here will have been more adequate than that for the other regions of blocks A–C on account of its heavier stocking, the figures may indicate that the shelter afforded by thin bracken is favourable for survival, as was found in America by W. F. McCullock (1942).

Douglas fir is always described as intolerant by American authors. When young it thrives well beneath the canopy of pine and oak however, and under these conditions its maximum height at 10 years is about 180 cm. (72 in.), and its average height 100 cm. (40 in.). The canopy also affords protection against frost; in the spring of 1943 about 40 % of the seedlings in the open were cut back by frost, while those under canopy escaped injury. In the sapling stage barking of the stem by deer appears to be the most serious danger. Douglas fir is very sensitive to this, and die-back or complete death follows removal of only a small part of the bark.

CONCLUSIONS AND DISCUSSION

American authors find a similar irregular periodicity in seed production to that indicated in the New Forest, good seed years usually occurring at intervals of 3–5 years (Allen, 1942; Haig, Davis & Weidman, 1941); indeed, a periodicity of this kind probably characterizes the majority of trees.

Establishment in the area studied seems to be largely determined by the presence of a carpet of coniferous litter, deciduous litter providing unsuitable conditions. Bare

mineral soil is also suitable, and after disturbance its presence might be an important factor in promoting regeneration. Several American authors (e.g. Larsen, 1924; Haig, 1936) have studied the effect of different kinds of substratum, including forest 'duff' of various kinds, on the germination and survival of Douglas fir. There is, however, no indication as to whether the duff used included litter from deciduous species. Fisher (1935) compared germination on various substrata under greenhouse conditions. Duff from several different sources was used, but no information is given as to how these differed from each other. Douglas fir germinated best on duff from an 'overmature virgin stand' of *Pinus monticola*, while duff from a 'virgin mixed stand' was amongst the poorest of the substrates. If the term 'mixed' here implies mixture with deciduous species, his figures confirm the findings of the present work.

In the pine and the pine-oak crop a carpet of bare litter or litter with moss and little higher vegetation seems to be necessary. When the canopy becomes sufficiently open to permit Douglas fir establishment other vascular plants also begin to invade, and in a few years further entry of Douglas fir becomes impossible. There will thus be a limited period in the development of the crop when a hitherto dense canopy is beginning to open during which conditions for regeneration are very favourable. In the absence of canopy open vegetation with much litter and moss also appears to be necessary, and coincidence of a good seed year with the year of felling would apparently be needed to give a good stocking of young Douglas fir.

The role of Douglas fir in Britain

It is interesting to speculate on the possible future for Douglas fir in British vegetation. In its shade-tolerance in youth it exceeds most British trees except *Fagus*. In rate of growth, on suitable soils, it is comparable when young with sycamore and birch, and this high rate is maintained longer, so that at the age of eighty it is usually much taller than any other British tree at maturity. In North America, it attains an age of many hundreds of years, and unless it proves susceptible in this country to butt rot or other form of disease, it should rival most of our indigenous trees in longevity. All these traits, coupled with its ability to regenerate on an organic substratum, appear to fit it for the role of a climax dominant. If, however, its behaviour in the New Forest is characteristic, it would only be able to enter our native woodland freely under the rather special conditions provided by the floor of a conifer crop or by the clearance of vegetation by felling, burning, etc. Very slow invasion might of course take place without these special conditions, and this would be assisted by its ability to regenerate on its own litter.

APPENDIX

Statistical examination of quadrat data

Comparisons have been made between the frequencies of cover classes in quadrats with seedlings and in quadrats without seedlings. For example, of the 157 quadrats without first-year seedlings in block D 138 (87%) had no litter while six (2·3%) had 80–100% litter. Of the thirty-seven quadrats with seedlings three (8·1%) had no litter, and sixteen (43·2%) had 80–100% litter, so that there is apparently an association between presence of seedlings and litter. The frequency distributions of the cover-classes of all the field-layer components for populations of quadrats with and without seedlings have been compared in this way, and the significance of the differences between them tested by χ^2. In the calculation of χ^2 it is always necessary to group some cover classes together on account of the small numbers of quadrats in them, and frequently it is only possible to use two groups, when a 2×2 contingency table results. The value of χ^2 may depend to a considerable extent on the boundaries chosen for the groups. Thus for the association of regeneration with moss in Shave Green $\chi^2 = 5\cdot7$ when comparison is made between quadrats with 25% or more moss cover and those with less. If 50% moss cover is taken as the boundary between the two groups however $\chi^2 = 1\cdot46$. The comparisons have been made for the following populations:

(1) Sixty-nine quadrats beneath pine in Shave Green Inclosure.
(2) 194 quadrats in all regions of block D.
(3) 491 quadrats in pine and pine-oak regions of blocks A–C.

Table 4 gives the results of the tests of significance. The figures for Shave Green relate to the presence of 1–4-year-old seedlings; the other figures relate to first-year seedlings only.

Table 4

| | Shave Green Unfelled pine | | | | Busketts Lawn | | | | | | | |
| | | | | | Unfelled, block D, all crops | | | | Felled, blocks A–C, pine and pine oak | | | |
	N	χ^2	P	Ass.	N	χ^2	P	Ass.	N	χ^2	P	Ass.
Pteridium	1	3·5	0·06	–	2	6·4	0·041	–	2	8·094	0·018	–
Molinia	1	0·95	0·3	.	1	6·786	0·009	–	3	7·2	0·068	–
Rubus fruticosus	1	4·9	0·029	+	2	15·3	0·001	–	3	0·48	0·5	.
Grass	,	.	.	.	1	0·0062	0·9	.	1	0·74	0·4	.
Herbs	.	.	.	.	2	4·058	0·1	.	.	.	.	.
Moss	1	5·7	0·018	+	2	3·259	0·2	–	2	4·77	0·09	+
Bare	.	.	.	.	1	21·07	0·001	+	1	2·78	0·09	+
Litter	2	7·02	0·03	+	1	96·01	0·001	+	2	3·16	0·2	.
Litter + Bare	.	.	.	.	2	20·92	0·001	+	.	.	.	.
Litter + Bare + Moss	1	15·5	0·001	+	3	14·02	0·003	+	3	12·77	0·005	+
Vaccinium myrtillus (25%)	1	15·3	0·001	–	.	.	.	.	.	.	.	.

$N =$ degrees of freedom.
$P =$ probability of chance occurrence of association.
Ass. = nature of the association, whether positive or negative.

Many of the differences between Shave Green and block D of Busketts Lawn are explicable by the fact that in the latter the majority of the seedlings are in the Douglas fir region which is almost devoid of ground vegetation. This explains the exceptionally strong association with litter. Since moss is practically absent in the Douglas crop but abundant beneath the pine, it appears slightly unfavourable, and association of seedlings with combined cover of litter plus moss is lower than that with litter alone. The antagonism to *Rubus* may also be partially explained in this way, but must also be largely due to the abundance of *Rubus* in the oak-pine region where litter conditions are unfavourable.

In the felled blocks A–C the relations appear to be similar. The most striking differences are the indifference of regeneration to *Rubus* and the decreased association with litter. The change with respect to *Rubus* may be due to the alterations in vegetation following felling. Before felling *Rubus* was associated more particularly with the heavy soils of the oak-pine region, and though widespread elsewhere formed

very little cover, so that it was present in only 58% of the quadrats in the pine and pine-oak regions. After felling it increased in abundance so that it was present in 73% of the quadrats in blocks A–C, but cover was still very low. The lack of sensitivity to litter is perhaps explicable by the much greater proportion of litter after felling (as a result of destruction of ground vegetation); obviously the more widespread favourable conditions, the less sharply will their influence be shown. In the unfelled crop 73% of the quadrats had no litter and 19·7% had 50% or more; in the felled crop 19·3% had no litter, and 45·9% had 50% or more.

REFERENCES

Allen, G. S. (1942). Douglas fir; a summary of its life history. *Brit. Columbia For. Serv. Res. note* 9.

Clapham, A. R. (1936). Over-dispersion in grassland communities and the use of statistical methods in plant ecology. *J. Ecol.* **24**, 242–51.

Fisher, G. M. (1935). Comparative germination of tree species on various kinds of surface-soil material in the western white pine type. *Ecology*, **16**, 606–11.

Haig, I. T. (1936). Factors controlling initial establishment of western white pine and associated species. *Bull. Yale Univ. Sch. Forestry*, no. 41.

Haig, I. T., Davis, K. P. & Weidman, R. H. (1941). Natural regeneration in the Western white pine type. *U.S.D.A. Tech. Bull.* 767.

Larsen, J. A. (1924). Some factors affecting reproduction after logging in Northern Idaho. *Journ. Ag. Res.* **28**, 1149–57.

McCullock, W. F. (1942). The role of bracken fern in Douglas fir regeneration. *Ecology*, **23**, 484–5.

Richardson, King, Driver, & Abraham (1787). A survey of the New Forest. The text is in MS.: the accompanying maps are printed.

SIXTH REPORT OF THE TRANSPLANT EXPERIMENTS OF THE BRITISH ECOLOGICAL SOCIETY AT POTTERNE, WILTSHIRE

BY ERIC M. MARSDEN-JONES AND W. B. TURRILL

The last published report of the Transplant experiments (*J. Ecol.* **26**, 359–79, 1938) dealt with results up to the end of 1937. This report gives and considers the results obtained for the three years 1938–40: the plant scorings to the end of 1940 and the meteorological data to the end of September 1940. The committee was compelled by circumstances outside its control to discontinue the experiments from the end of 1940.

Transplant experiments with *Silene maritima* were completed in 1938, and the plots previously occupied by this species were used for *Solanum dulcamara* var. *marinum*.

METEOROLOGICAL DATA

The total annual rainfall for 1938 was 578·25 mm. (23·53 in.), for 1939 was 760·50 mm. (30·42 in.), and for the first nine months of 1940 was 362·75 mm. (14·51 in.). There were 156 'rain days' in 1938, 164 in 1939, and 90 in the first nine months of 1940.

Meteorological data

1938		Temperature				Relative humidity		Rainfall			
		Max.		Min.				Rainfall in mm.		No. of rain days	
		° C.	° F.	° C.	° F.	Max.	Min.	Week	Month	Week	Month
1–7	Jan.	6·1	43	− 1·1	30	94	51	4·75		5	
8–14		10·0	50	− 1·1	30	94	63	26·75		7	
15–21		10·0	50	0·6	33	95	42	10·5		4	
22–28		11·7	53	− 1·1	30	95	37	11·0		5	
29–31		10·0	50	1·7	35	95	52	7·5	60·50	3	24
1–7	Feb.	9·4	49	0·6	33	95	50	0·75		1	
8–14		9·4	49	− 3·3	26	95	32	2·25		3	
15–21		8·3	47	− 1·1	30	95	44	2·0		1	
22–28		12·8	55	− 2·2	28	95	33	12·0	17·00	4	9
1–7	Mar.	18·3	65	− 5·6	22	95	10	0·0		0	
8–14		16·1	61	0·0	32	95	18	0·0		0	
15–21		17·2	63	2·2	36	95	19	0·0		0	
22–28		18·3	65	− 1·1	30	95	20	2·25		2	
29–31		15·0	59	5·6	42	95	36	0·0	2·25	0	2
1–7	Apr.	19·4	67	− 4·4	24	95	13	2·0		1	
8–14		18·3	65	− 5·0	23	95	15	0·0		0	
15–21		15·6	60	− 7·8	18	95	16	0·0		0	
22–28		16·1	61	− 3·3	26	95	18	0·75		1	
29–30		14·4	58	0·0	32	88	19	0·0	2·75	0	2
1–7	May	19·4	67	− 4·4	24	95	16	5·0		2	
8–14		19·4	67	1·1	34	95	10	2·0		2	
15–21		23·9	75	− 2·2	28	95	17	0·0		0	
22–28		24·4	76	3·3	38	95	19	16·0		4	
29–31		12·8	55	5·6	42	95	46	12·5	35·50	3	11
1–7	June	21·1	70	5·6	42	95	20	11·5		4	
8–14		25·6	78	2·2	36	95	26	0·25		1	
15–21		28·9	84	5·6	42	95	18	0·25		1	
22–28		21·1	70	11·1	52	95	32	7·5		3	
29–30		18·3	65	3·3	38	95	26	2·5	22·00	1	10

Meteorological data (continued)

		Temperature				Relative humidity		Rainfall in mm.		No. of rain days	
		Max.		Min.							
1938		° C.	° F.	° C.	° F.	Max.	Min.	Week	Month	Week	Month
1–7	July	21·7	71	2·2	36	95	22	27·75		5	
8–14		21·7	71	5·6	42	95	30	19·0		4	
15–21		26·7	80	6·7	44	95	27	8·25		1	
22–28		27·8	82	8·9	48	95	26	14·25		2	
29–31		23·9	75	12·2	54	95	56	0·0	69·25	0	12
1–7	Aug.	29·4	85	11·1	52	95	26	9·5		2	
8–14		25·0	77	5·6	42	95	29	1·75		2	
15–21		23·3	74	3·3	38	95	25	10·0		5	
22–28		22·8	73	8·9	48	95	38	26·0		4	
29–31		19·4	67	2·2	36	95	23	0·0	47·25	0	13
1–7	Sept.	18·9	66	1·1	34	95	22	4·25		2	
8–14		26·1	79	4·4	40	95	37	1·0		1	
15–21		18·9	66	1·7	35	95	20	15·5		3	
22–28		21·1	70	6·7	44	95	35	19·0		5	
29–30		20·0	68	7·8	46	92	48	18·75	58·50	2	13
1–7	Oct.	13·3	56	4·4	40	94	35	69·75		7	
8–14		16·1	61	4·4	40	95	43	10·25		4	
15–21		15·6	60	2·8	37	94	29	8·75		4	
22–28		14·4	58	0·6	33	95	35	4·5		2	
29–31		12·2	54	0·6	33	92	61	6·5	99·75	2	19
1–7	Nov.	14·4	58	3·9	39	93	32	4·0		3	
8–14		15·0	59	6·7	44	94	51	9·75		4	
15–21		12·8	55	− 0·6	31	92	50	27·5		6	
22–28		12·2	54	0·0	32	95	41	32·5		5	
29–30		9·4	49	1·1	34	93	48	9·5	83·25	2	20
1–7	Dec.	12·2	54	− 0·6	31	95	55	6·75		6	
8–14		10·6	51	− 2·2	28	93	58	38·25		5	
15–21		9·4	49	− 7·8	18	92	34	13·5		3	
22–28		6·7	44	− 3·3	26	93	61	14·25		5	
29–31		8·9	48	0·0	32	93	50	7·5	80·25	2	21
1939											
1–7	Jan.	11·7	53	− 5·0	23	92	55	14·25		5	
8–14		11·1	52	− 2·2	28	95	43	18·0		3	
15–21		10·6	51	2·2	36	95	54	33·75		7	
22–28		7·2	45	− 1·1	30	94	42	47·0		5	
29–31		2·2	36	− 1·1	30	92	53	0·0	113·0	0	20
1–7	Feb.	11·7	53	− 5·0	23	95	44	6·0		2	
8–14		12·2	54	0·6	33	95	40	3·75		2	
15–21		11·7	53	− 1·7	29	93	30	5·25		2	
22–28		8·9	48	− 4·4	24	95	35	14·75	29·75	4	10
1–7	Mar.	13·3	56	1·1	34	95	27	10·0		3	
8–14		12·2	54	− 2·2	28	95	31	12·75		4	
15–21		10·6	51	− 1·7	29	95	33	4·25		2	
22–28		10·0	50	− 3·3	26	95	32	4·75		4	
29–31		16·7	62	− 0·6	31	95	26	0·0	31·75	0	13
1–7	Apr.	17·2	63	0·0	32	95	32	23·75		5	
8–14		24·4	76	0·6	33	95	18	5·75		2	
15–21		21·1	70	− 0·6	31	95	10	2·0		1	
22–28		11·7	53	− 2·8	27	95	24	13·25		4	
29–30		11·1	52	2·8	37	95	27	21·5	66·25	2	14
1–7	May	18·9	66	1·7	35	93	28	15·5		4	
8–14		22·8	73	2·7	36	95	18	1·5		2	
15–21		17·8	64	5·0	41	95	19	6·0		3	
22–28		27·2	81	4·4	40	95	16	0·0		0	
29–31		26·1	79	5·0	41	95	19	0·0	23·0	0 ·	9
1–7	June	28·9	84	8·9	48	94	10	7·25		2	
8–14		25·6	78	3·3	38	93	10	7·5		3	
15–21		18·9	66	6·1	43	93	23	37·0		5	
22–28		20·9	68	5·6	42	90	26	10·5		3	
29–30		26·1	79	6·1	43	92	24	0·0	62·25	0	13

Meteorological data (continued)

1939		Max. °C	Max. °F	Min. °C	Min. °F	RH Max.	RH Min.	Rain mm Week	Rain mm Month	Rain days Week	Rain days Month
1–7	July	20·6	69	5·6	42	90	14	24·0		4	
8–14		21·1	70	4·4	40	90	26	23·25		3	
15–21		20·0	68	8·3	47	86	46	44·75		7	
22–28		21·7	71	5·6	42	89	31	19·5		6	
29–31		20·0	68	11·1	52	88	41	9·25	120·75	3	23
1–7	Aug.	21·1	70	8·9	48	88	31	38·0		5	
8–14		22·2	72	6·1	43	90	19	3·75		2	
15–21		27·8	82	11·1	52	90	26	0·75		1	
22–28		26·7	80	10·0	50	89	31	7·25		3	
29–31		27·8	82	13·3	56	88	24	0·0	49·75	0	11
1–7	Sept.	25·6	78	10·0	50	89	23	25·25		3	
8–14		25·0	77	5·6	42	89	29	3·75		1	
15–21		26·7	80	9·4	49	90	34	0·0		0	
22–28		18·3	65	2·2	36	94	23	0·0		0	
29–30		18·3	65	2·8	37	87	25	0·0	29·0	0	4
1–7	Oct.	17·8	64	2·2	36	70	28	9·0		3	
8–14		16·1	61	3·3	38	87	36	41·75		5	
15–21		13·9	57	− 2·8	27	88	23	11·75		2	
22–28		12·8	55	− 1·1	30	88	27	7·0		5	
29–31		8·9	48	− 1·1	30	85	50	7·5	77·0	3	18
1–7	Nov.	13·9	57	5·6	42	88	47	31·0		6	
8–14		13·9	57	4·4	40	89	49	11·75		3	
15–21		12·2	54	− 2·2	28	88	44	23·25		4	
22–28		17·2	53	− 1·7	29	86	46	41·25		6	
29–30		12·2	54	11·1	52	86	63	5·75	113·0	2	21
1–7	Dec.	12·2	54	− 4·4	24	88	50	30·0		4	
8–14		11·1	52	0·0	32	86	56	8·75		2	
15–21		8·9	48	− 7·8	18	85	41	1·0		1	
22–28		6·7	44	− 8·3	17	86	46	5·25		1	
29–31		3·9	39	− 9·4	15	82	57	0·0	45·0	0	8
1940											
1–7	Jan.	9·4	49	− 5·6	22	87	37	3·5		2	
8–14		6·1	43	− 11·1	12	86	38	0·0		0	
15–21		1·1	34	− 16·7	2	85	33	0·0		0	
22–28		5·0	41	− 11·1	12	86	27	39·0		4	
29–31		0·0	32	− 5·6	22	82	62	8·0	50·5	2	8
1–7	Feb.	8·9	48	− 1·7	29	82	60	30·25		6	
8–14		6·1	43	− 8·9	16	82	31	0·0		0	
15–21		11·7	53	− 11·1	12	87	53	16·0		4	
22–28		11·1	52	0·0	32	87	48	10·25		4	
29		1·1	34	− 0·6	31	87	24	4·5	61·0	1	15
1–7	Mar.	11·7	53	− 7·2	19	89	11	0·0		0	
8–14		17·2	63	− 3·9	25	89	22	11·75		2	
15–21		12·8	55	− 0·6	31	86	31	24·75		4	
22–28		13·9	57	− 4·4	24	86	14	2·5		3	
29–31		14·4	58	2·8	37	86	29	1·75	40·75	1	10
1–7	Apr.	14·4	58	− 2·8	27	89	20	4·25		4	
8–14		13·3	56	− 5·6	22	88	18	2·75		3	
15–21		17·8	64	− 3·9	25	89	16	24·25		4	
22–28		25·0	77	3·9	39	88	14	20·25		5	
29–30		15·0	59	5·6	42	87	30	8·0	59·5	1	17
1–7	May	20·6	69	3·9	39	87	17	0·0		0	
8–14		19·4	72	1·7	35	89	16	11·5		1	
15–21		22·8	73	0·6	33	87	19	5·5		2	
22–28		24·4	76	6·1	43	88	19	5·75		3	
29–31		22·2	72	7·8	46	88	26	9·75	32·5	1	7

Meteorological data (continued)

1940	Temperature Max. °C.	Max. °F.	Min. °C.	Min. °F.	Relative humidity Max.	Min.	Rainfall Rainfall in mm. Week	Month	No. of rain days Week	Month
1-7 June	33·3	92	8·9	48	87	9	0·0		0	
8-14	33·3	92	6·7	44	88	10	0·5		1	
15-21	31·1	88	7·8	46	88	10	4·75		3	
22-28	24·4	76	7·2	45	85	20	7·25		4	
29-30	25·6	78	6·7	44	86	10	0·5	13·0	1	9
1-7 July	29·4	85	7·2	45	85	10	2·75		2	
8-14	22·2	72	7·2	45	84	11	52·0		5	
15-21	21·7	71	7·8	46	83	23	12·0		5	
22-28	23·3	74	5·0	41	85	18	7·5		2	
29-31	25·6	78	10·6	51	85	21	0·0	74·25	0	14
1-7 Aug.	28·3	83	8·3	47	85	15	0·0		0	
8-14	24·4	76	7·8	46	85	13	3·5		1	
15-21	26·1	79	5·6	42	86	13	0·0		0	
22-28	23·9	75	5·6	42	85	11	0·0		0	
29-31	26·7	80	5·0	41	85	16	0·0	3·5	0	1
1-7 Sept.	28·9	84	5·6	42	84	11	0·0		0	
8-14	18·3	65	2·8	37	84	10	11·75		4	
15-21	20·0	68	4·4	40	83	16	15·25		4	
22-28	18·9	66	0·6	33	83	19	0·75		1	
29-30	11·1	52	5·0	41	83	39	0·0	27·75	0	9

Drought of the summer of 1940

There were some rather marked effects of the dry periods in the summer of 1940, but, as shown by scorings to the end of the year, these were mostly temporary. The following were noted:

Centaurea. Wilting of basal leaves was most obvious on sand; it was relatively slight on calcareous sand and clay; no wilting was observed on chalky clay and Potterne soil. All wilted ramets recovered completely and quickly after rain.

Plantago. No wilting occurred in August, but on all soils the older leaves showed considerable development of purple anthocyanin. Later (12. ix. 40), on Potterne soil, chalky clay, and clay, many of the outer leaves wilted and died off, while on sand and calcareous sand few leaves were affected.

Fragaria. Certain outer leaves dried up, especially on chalky clay, calcareous sand, and sand.

Solanum dulcamara var. *marinum.* There was undue leaf-fall from ramets on clay, chalky clay, and Potterne soil, but little other effect was observed.

Phleum pratense. Withering and browning of leaves were least on Potterne soil, but were more marked in the sequence on sand, calcareous sand, clay, and (most) chalky clay.

Phleum nodosum. Withering and browning of leaves were least marked on clay, but were more marked in the sequence on chalky clay, sand, calcareous sand, and (most) Potterne soil.

The great ice storm of 28. i. 40 did not appear to have damaged the plants on any of the plots. The very favourable spring that followed was probably the main cause of some peculiarities in flowering and fruiting noted for a number of the species.

BIOTIC FACTORS

Slug damage was negligible or absent on all plots for all three years.

Grasshoppers maintained themselves on *Phleum nodosum* ramets on Potterne soil, but did no noticeable damage to the plants.

In all three years most moss growth occurred on calcareous sand, then, in descending order of abundance, on sand, Potterne soil, and the clays. *Cladonia* was very abundant on sand except on the *Centaurea* plot, where there was none till 1940, and was most abundant on the *Phleum* plots. *Cladonia* was not observed on the other soils till 1940, when it was found in small patches on clay and Potterne soil.

Centaurea nemoralis Jord. forma radiata albiflora

Seasonal conditions and deaths. The only additional deaths to record were No. 81 on chalky clay and Nos. 146 and 150 A on Potterne soil, all three in 1940. Thus in 13 years the following ramet deaths have occurred:

Soil	Ramets	Deaths
Sand	26	0
Calcareous sand	26	0
Clay	26	8
Chalky clay	26	7
Potterne soil	26 (+5)	5 (+5)
	130 (135)	20 (25)

Adding 5 to each figure for Potterne soil, to account for replacements in 1931, the ratio for living ramets to total ramets used, is, after 13 years, 0·81 : 1, and the ratio of total ramets used to total deaths during the same period is 5·4 : 1. The greater number of deaths was due to rotting resulting from overcrowding of centrally placed ramets following lush growth of the marginally situated ramets. Primary spring growth commenced early in 1938 and 1939 and was marked on all soils by 13. ii. 38. On 5. ii. 39 and 11. iii. 40 the sequence (most growth first) was: clay, chalky clay, sand, calcareous sand, Potterne soil. For 21. xii. 39 and 19. xi. 40, the sequence for winter growth (best first) was: chalky clay, clay, sand, Potterne soil, calcareous sand. There has been no alteration in the erect habit of the stems on any of the soils, but at Kew the stock retained the ascending stems.

Seedlings	13. ii. 38	24. iv. 38	12. viii. 38	20 x. 38
Sand	Few	Very numerous	Very numerous	Very numerous
Calcareous sand	Very few	Very numerous	Numerous	Very numerous
Clay	None	Numerous	Few	Few
Chalky clay	Very few	Very numerous	Numerous	Numerous
Potterne soil	None	Numerous	Numerous	Numerous

	5. ii. 39	10. iv. 39	16. x. 39	17. iv. 40
Sand	None	Few	Few	Very few
Calcareous sand	None	Very numerous	Very numerous	Numerous
Clay	None	Few	None	Numerous
Chalky clay	None	Numerous	Very few	Very numerous
Potterne soil	None	Few	None	Very few

	20. ix. 40	26. ix. 40	17. xi. 40	
Sand	None	Few	Very few	
Calcareous sand	Very few	Numerous	Very few	
Clay	None	Very few	Very few	
Chalky clay	Very few	Numerous	Very few	
Potterne soil	None	Few	Very few	

The scoring for 26. ix. 40 was made a few days after rain fell and shows the effect of rain when compared with the scoring for 20. ix. 40.

General tone. Sand maintained the first place throughout the three years. There was fluctuation in the sequence of tone on the other soils with a tendency for general improvement (apart from deaths) on the clays and Potterne soil. The sequence at the final scoring (26. ix. 40) was (best first): sand, calcareous sand, chalky clay, clay, Potterne soil. The natural cloning on all soils had by the spring of 1939 practically reached its limit from the original centres. Most had occurred on sand, then, in descending sequence, on clay, calcareous sand, chalky clay, Potterne soil.

Stem heights (maximum for every soil, in dm.)

	23. viii. 39	19. viii. 40
Sand	8·3	7·7
Calcareous sand	8·3	7·4
Clay	9·0	8·2
Chalky clay	9·8	8·4
Potterne soil	6·5	8·3

Number of flowering stems per ramet

	Sand			Calcareous sand			Clay			Chalky clay			Potterne soil		
	1938	1939	1940	1938	1939	1940	1938	1939	1940	1938	1939	1940	1938	1939	1940
Total ramets	26	26	26	26	26	26	18	18	18	20	20	19	23	23	21
Total stems per soil	2111	2331	2090	1653	1824	1620	1080	1073	1045	1393	1390	1283	761	721	619
Max. per ramet	145	205	168	157	172	156	107	112	107	125	120	104	87	83	73
Min. per ramet	24	22	35	18	18	17	25	34	29	10	10	11	4	4	0
Mean per ramet	81·2	89·7	80·4	63·6	70·2	62·3	60·0	59·6	58·1	69·6	69·5	67·5	33·1	31·3	29·5
Standard deviation	32·9	44·6	35·2	41·1	44·5	40·4	21·4	20·6	19·0	31·0	28·6	26·4	18·7	19·5	20·4

The regularities shown by the figures for numbers of flowering stems in *Centaurea* are instructive and suggest that the character though simple is a valid criterion of soil influence. The total number of stems per soil and the mean per ramet are uniformly highest on sand, quantitatively in agreement with our qualitative scoring for 'general tone'. In these respects the plants on Potterne soil definitely occupy the lowest position and, except for 'mean per ramet' for 1939, were still, up to 1940, slightly on the downgrade for total ramets, total stems per soil, maximum and minimum per ramet, and mean per ramet, with regular increase in variation between the ramets as shown by increase in the values of standard deviation from the mean. The importance of this result, which has become increasingly evident from the early years of the experiments, is linked with the two facts: (1) that the sand is, as shown by the chemical analyses, the poorest of the soils in the usual plant foods, and (2) that all the other species of plants grown on the five soils behave relatively very differently and, mostly, a low, and often the lowest, place in tabulated scorings for various characters is occupied by the ramets growing on sand. The higher standard deviations shown on sand and calcareous sand than on the other soils is due largely to the effects of shading of ramets near the centre of the beds by the denser growth of the more external ramets correlated with the fact that none of the ramets on the sands have died.

Primary flowering. Maximum flowering on all soils was scored for 12. vii. 38, 4. vii. 39, and 23. vii. 40.

Completion of primary flowering. The sequence (the first completed placed first) was: (25. vii. 38 and 24. vii. 39) calcareous sand, sand, chalky clay, clay, Potterne soil; (24. vii. 40) calcareous sand, clay, chalky clay, sand, Potterne soil.

Biotic factors. On 11. vi. 38 a black fly attack was noted on 7 ramets on sand and 1 ramet on calcareous sand, but the attack was not severe. Slugs attacked basal leaves on clay only (5. ii. 39). On sand and calcareous sand ramets in the centre of the plots were tending to be smothered by growth of *Brachythecium* (5. ii. 39).

First flowering

	1938					1939					1940				
	Sand	Cal-careous sand	Clay	Chalky clay	Pot-terne soil	Sand	Cal-careous sand	Clay	Chalky clay	Pot-terne soil	Sand	Cal-careous sand	Clay	Chalky clay	Pot-terne soil
6 June	—	—	—	—	—	—	—	—	—	—	2	2	—	—	—
7	—	—	—	—	—	—	—	—	—	—	7	10	—	2	3
8	—	—	—	—	—	—	—	—	—	—	8	20	3	7	5
9	—	—	—	—	—	—	—	—	—	—	18	22	8	13	7
10	—	—	—	—	—	—	—	—	—	—	23	24	13	17	11
11	—	—	—	—	—	—	—	—	—	—	25	25	15	17	15
12	—	—	—	—	—	—	—	—	—	—	26	26	17	19	19
13	—	—	—	—	—	—	1	—	—	—	—	—	—	—	19
14	—	—	—	—	—	1	1	—	—	—	—	—	—	—	20
15	—	—	—	—	—	1	1	—	1	2	—	—	—	—	21
16	—	—	—	—	—	1	3	—	2	2	—	—	—	—	—
17	—	—	—	—	—	3	5	—	3	2	—	—	—	—	—
18	—	—	—	—	—	4	5	—	4	2	—	—	—	—	—
19	—	—	—	—	—	4	5	1	4	5	—	—	—	—	—
20	—	—	—	—	—	7	9	2	4	6	—	—	—	—	—
21	—	1	—	—	—	7	10	3	6	9	—	—	—	—	—
22	—	2	—	—	—	10	14	3	7	9	—	—	—	—	—
23	—	2	—	—	—	14	18	8	14	9	—	—	—	—	—
24	—	4	—	—	—	15	20	11	15	11	—	—	—	—	—
25	—	5	—	2	1	18	24	13	16	12	—	—	—	—	—
26	1	13	—	3	1	22	25	15	16	15	—	—	—	—	—
27	8	21	—	4	5	25	26	18	19	17	—	—	—	—	—
28	14	23	3	7	8	26	—	—	20	18	—	—	—	—	—
29	18	24	5	14	9	—	—	—	—	19	—	—	—	—	—
30	22	24	6	14	9	—	—	—	—	20	—	—	—	—	—
1 July	25	25	11	15	11	—	—	—	—	22	—	—	—	—	—
2	25	26	15	16	12	—	—	—	—	22	—	—	—	—	—
3	25	—	15	18	14	—	—	—	—	22	—	—	—	—	—
4	25	—	16	18	16	—	—	—	—	23	—	—	—	—	—
5	25	—	17	18	17	—	—	—	—	—	—	—	—	—	—
6	25	—	18	19	19	—	—	—	—	—	—	—	—	—	—
7	25	—	—	—	19	—	—	—	—	—	—	—	—	—	—
8	26	—	—	—	21	—	—	—	—	—	—	—	—	—	—
9	—	—	—	—	22	—	—	—	—	—	—	—	—	—	—

Silene maritima L.—*narrow-leaved variety*

Experiments were continued for one more year (1938) with this species.

Deaths. Nos. 6, 11, 13 died during the spring of 1938 and Nos. 10, 17, 18, 20, 23, 25, and 25 A died during the summer of 1938. Thus on sand the only ramets remaining alive after three years were Nos. 21, 22, and 24. On all the other soils all ramets (26 per plot) survived till the end of the experiment with this species. Death of ramets on the sand was due to root-rot.

Habit and foliage. There was no change in general habit or gross morphological characters on any of the soils, except that the leaves were slightly smaller on sand. By February, on all plots about equally, the old leaves had died and fallen off but the shoot tips were alive and showed some development of small young leaves. By April, some of the branches had been killed back, especially on chalky clay and then, in order, on Potterne soil, clay, sand, and calcareous sand. There was some new growth, with flower buds, from the centre

of the ramets: most occurred on calcareous sand, then, in order, on sand, Potterne soil, chalky clay, and clay.

General tone. Throughout the year, with very slight fluctuations, the sequence (best first) was: chalky clay, clay, Potterne soil, calcareous sand, sand.

First flowering (1938)

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
29 April	—	—	—	—	2 .
30	—	—	—	—	2
1 May	—	—	—	—	2
2	1	—	—	—	2
3	1	—	—	—	3
4	1,	—	—	—	3
5	1	—	—	—	3
6	1	—	—	—	3
7	2	1	—	—	3
8	2	1	—	—	3
9	2	1	—	—	3
10	3	1	—	—	3
11	4	2	—	—	4
12	4	2	—	—	4
13	4	3	—	1	4
14	4	4	—	1	4
15	4	5	—	1	5
16	5	7	—	1	5
17	5	7	—	2	5
18	5	8	—	2	6
19	5	11	—	2	6
20	5	11	—	4	7
21	5	12	2	4	7
22	5	12	2	5	7
23	6	17	6	10	9
24	6	17	7	12	12
25	7	19	9	18	12
26	7	20	12	20	12
27	7	21	13	22	15
28	7	21	14	22	15
29	7	21	15	23	19
30	7	23	15	24	19
31	7	23	17	24	19
1 June	7	23	19	24	20
2	7	23	20	24	20
3	7	24	22	26	22
4	7	24	22	—	22
5	7	24	24	—	24
6	8	25	24	—	24
7	—	25	26	—	25
8	—	25	—	—	25
13	—	25	—	—	26
14	—	26	—	—	—

Late flowering. On 20. x. 38 there were three ramets on calcareous sand and three on chalky clay with late flowers at full anthesis. No ramets on other soils then had flowers.

Seedlings

	13. ii. 38	24. iv. 38	12. viii. 38	20 x. 38
Sand	Very few	Numerous	Few	Few
Calcareous sand	None	Very few	Few	None
Clay	None	None	None	None
Chalky clay	None	None	None	None
Potterne soil	None	None	None	None

A factor affecting the production of seeds was that the clone was essentially female, though extremely rarely a very few stamens were produced with pollen. For first flowers, two ramets on chalky clay and one on Potterne soil had 'hermaphrodite' flowers with

two to five stamens. Numerous and very diverse stocks of both *Silene maritima* and *S. vulgaris* were flowering in the Experimental Ground in 1938 within easy range of insect flight to the Transplant Beds. That out-breeding played a most important part in the production of the seedlings recorded is confirmed by an analysis of young seedlings. Scoring the first foliage leaves into three groups, narrow, intermediate, and broad, the following figures were obtained:

17. x. 39	Narrow 35	Intermediate 58	Broad 19
17. x. 40	Narrow 3	Intermediate 3	Broad 3

The 'narrow'-leaved seedlings may or may not have been the results of selfings within the clone, the remainder were certainly not. The seedlings also showed a wide range of anthocyanin development (from very much to none). This, again, was due to mixed out-breeding.

A factor detrimental to the germination of seeds and establishment of seedlings was the dense growth of prostrate branches and foliage ('top hamper'). This was particularly obvious on the clays and Potterne soil during most of the year, though seedlings appeared on these plots after they had been cleared.

Root structure (5. xi. 38). *Sand.* Three to six main roots going down rather straight into the soil and branching profusely. These originate immediately below the crown. Hemicryptophytic shooting only just commencing. Superficial colour of washed roots: Clay Color (Ridgway, *Color Standards*, Pl. XXIX).

Calcareous sand. Five to six main roots spreading obliquely into the soil and branching profusely. These originate immediately below the crown and at 2–5 cm. depth below the soil surface the root branches are coiled about one another. Hemicryptophytic shooting slightly more advanced than on sand. Superficial colour of washed roots: Antimony Yellow (Ridgway, *Color Standards*, Pl. XX).

Clay. Five to ten main roots spreading horizontally or slightly obliquely into the soil and branching profusely. These originate immediately below the crown and there is some coiling at 2 cm. below ground level. Hemicryptophytic shooting more advanced than in calcareous sand. Superficial colour of washed roots: Honey Yellow (Ridgway, *Color Standards*, Pl. XXX).

Chalky clay. Seven to eleven main roots spreading down obliquely, at a more acute angle with the soil surface than in calcareous sand but less so than in clay, and branching profusely. These originate immediately below the crown. There is some coiling 1–5 cm. below the soil level. Hemicryptophytic shooting is the most advanced of that on all soils. Superficial colour of washed roots: Honey Yellow (Ridgway, *Color Standards*, Pl. XXX).

Potterne soil. Six to nine main roots spreading obliquely into the soil and branching profusely. These originate 3–4 cm. below the surface of the soil. There is some coiling at 5 to 6 cm. depth. Hemicryptophytic shooting only just commencing but is slightly more advanced than on sand. Superficial colour of washed roots: Honey Yellow (Ridgway, *Color Standards*, Pl. XXX).

Plantago major L.—*large variety*

Deaths. In 1938, on sand, No. 10 died. No more deaths occurred in 1939. In the summer of 1940 the following deaths occurred: on sand, Nos. 1, 2, 3, 5, 6, 8, 9, 12, 13; on calcareous sand, Nos. 31, 37; on clay, Nos. 56, 58, 60, 62.

General tone (best first)

11. iv. 38 and 12. vii. 38	17. x. 38	10. iv. 39	9. viii. 39	23. x. 39, 9. v. 40, 17. vii. 40 and 15. ix. 40
Potterne soil	Chalky clay	Chalky clay	Chalky clay	Chalky clay
Clay	Clay	Potterne soil	Clay	Potterne soil
Chalky clay	Potterne soil	Clay	Potterne soil	Clay
Calcareous sand	Calcareous sand	Calcareous sand	Calcareous sand	Calcareous sand
Sand	Sand	Sand	Sand	Sand

Mildew. This was pronounced on many plants on Potterne soil in 1938. In 1939 and 1940 the plots remained clear of mildew but *Ramularia plantaginea* attacked the leaves in both years, especially on the clays and Potterne soil.

Indumentum and foliaceous bracts. These remained essentially as in the last scorings.

Seedlings

	13. ii. 38	11. viii. 38	17. x. 38	10. iv. 39
Sand	Very few	Very few	None	None
Calcareous sand	None	Numerous	Numerous	None
Clay	None	Numerous	None	None
Chalky clay	Very few	Very numerous	Numerous	None
Potterne soil	None	Very numerous	None	None

	20. v. 39	9. viii. 39	16. x. 39	19. iii. 40
Sand	Numerous	Very numerous	None	None
Calcareous sand	Numerous	Very numerous	Numerous	None
Clay	None	Very few	None	None
Chalky clay	Numerous	Numerous	Few	None
Potterne soil	Numerous	Very few	Very few	None

	17. iv. 40	15. ix. 40	17. xi. 40
Sand	Few	Numerous	None
Calcareous sand	Very few	Very numerous	None
Clay	Very few	None	Very few
Chalky clay	None	Numerous	None
Potterne soil	Very numerous	Numerous	None

Germination. Seed was collected from no. 51 (on clay) after open pollination and sown in pots of the five soils on 25. iv. 38. Germination was first on Potterne soil, then, in order, on sand, calcareous sand, clay, chalky clay. Best final germination was on Potterne soil, then, in order, on clay, sand, calcareous sand, chalky clay. The largest seedlings developed on Potterne soil, then, in order, on clay, calcareous sand, sand, chalky clay.

Infructescences. Observations made in the winter of 1939–40 suggest that frost increases the number of capsules dehiscing in winter.

Commencement of winter rest period. The sequence (earliest 'dormant' first) was, for 1939, sand, calcareous sand, chalky clay, clay, Potterne soil, and, for 1940, sand, clay, Potterne soil, calcareous sand, chalky clay.

Commencement of spring growth. The sequence (earliest first), recorded on 3. iv. 38 and 11. iii. 40 was Potterne soil, clay, chalky clay, calcareous sand, sand.

Retention of depth. None of the plants showed heaving up ('lifting') after frost or other weather changes on any of the soils. Stones and soils became heaped up around the ramets especially on calcareous sand.

Habit. Full records have been kept of the behaviour of individual ramets throughout the three years. A good deal of fluctuation has been noted but the general tendency has been for ramets on sand to develop a flat or semi-strict habit, those on calcareous sand a semi-strict to strict habit, and those on the clays and Potterne soil a strict habit.

Diameters of ramets, in cm.

11. viii. 38	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Max. diameter	46	46	93	88	94
Min. diameter	14	26	45	26	42
Mean diameter	32·2	33·9	72·3	63·9	64·8

23. viii. 39					
Max. diameter	32	45	113	98	84
Min. diameter	10	24	46	31	37
Mean diameter	18·2	36·3	77·9	71·4	63·9

5. viii. 40					
Max. diameter	30	55	77	93	80
Min. diameter	10	18	17	31	33
Mean diameter	26·0	31·9	52·3	60·8	63·2

Height of vegetative parts, in cm.

11. viii. 38	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Max. height	20	18	48	39	45
Min. height	6	6	16	17	22
Mean height	12·9	10·0	32·1	28·4	28·6

23. viii. 39					
Max. height	9	17	49	51	42
Min. height	4	6	15	12	19
Mean height	5·3	13·1	35·2	35·9	27·2

5. viii. 40					
Max. height	11	19	39	38	27
Min. height	4	5	9	8	6
Mean height	8·0	9·3	24·7	29·3	20·9

Number of crowns (rosettes) per ramet

3. iv. 38	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	13	13	14	14	14
Maximum	10	6	14	22	27
Minimum	1	1	3	7	4
Mean	5·2	4·5	8·5	14·7	1·1
Total per soil	68	58	119	206	159

13. iii. 39					
Number of ramets	12	13	14	14	14
Maximum	12	6	15	19	25
Minimum	1	1	2	6	4
Mean	4·9	4·5	7·9	14·7	10·3
Total per soil	59	59	111	206	144

17. iv. 40					
Number of ramets	3	12	14	14	14
Maximum	7	7	12	24	34
Minimum	3	1	1	6	3
Mean	5·3	4·6	6·6	15·3	12·8
Total per soil	16	56	93	214	179

Number of flowering spikes per ramet

1938	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	12	13	14	14	14
Maximum	35	40	108	111	103
Minimum	0	8	41	14	22
Mean	14·9	20·5	64·0	75·7	48·8
Standard deviation	12·4	10·5	18·8	26·5	17·4
Total per soil	179	267	896	1060	683

1939	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	9	13	14	14	14
Maximum	6	25	100	101	86
Minimum	0	5	27	13	13
Mean	2·2	15·8	64·0	61·7	44·3
Standard deviation	3·2	7·1	20·8	26·1	15·4
Total per soil	20	205	896	864	620

1940	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	3	12	12	14	14
Maximum	27	35	114	106	82
Minimum	10	8	7	21	8
Mean	19·3	16·9	61·4	65·6	48·6
Standard deviation	8·6	9·0	35·6	24·9	19·4
Total per soil	58	203	737	919	680

Height of flowering stems per ramet, in cm.

1938	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	10	13	14	14	14
Maximum	44	45	82	70	64
Minimum	20	25	44	33	36
Mean	33·4	33·5	63·2	55·4	47·1
Standard deviation	6·3	6·7	10·7	9·7	9·3

1939	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	5	13	14	14	14
Maximum	25	41	76	72	61
Minimum	15	14	32	23	35
Mean	17·6	31·2	61·4	58·4	50·1
Standard deviation	4·2	7·3	12·5	12·0	6·1

1940	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	3	12	12	14	14
Maximum	28	44	54	64	52
Minimum	16	15	10	19	5
Mean	23·3	27·5	36·5	51·5	38·9
Standard deviation	6·4	9·5	14·0	13·5	12·5

	1938					1939					1940				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
15 June	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—
16	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—
17	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—
18	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—
19	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—
20	—	—	—	—	—	—	—	—	—	—	—	—	6	—	—
21	—	—	—	—	—	—	—	—	—	—	—	—	6	—	—
22	—	—	—	—	—	—	—	—	—	—	—	—	6	1	—
23	—	—	—	—	—	—	—	—	—	—	—	—	7	3	—
24	—	—	—	—	—	—	—	—	—	—	—	—	8	3	—
25	—	—	—	—	—	—	—	—	—	—	—	—	9	3	—
26	—	—	—	1	—	—	—	—	—	—	—	—	9	3	—
27	—	—	—	1	—	—	—	—	—	—	—	—	11	5	—
28	—	—	—	1	—	—	—	—	—	—	—	—	12	6	—
29	—	—	—	2	—	—	—	1	—	—	—	1	—	7	—
30	—	—	—	3	—	—	—	1	—	—	—	2	—	11	—
1 July	—	—	—	3	—	—	—	1	—	—	—	2	—	14	1
2	—	—	—	3	—	—	1	1	—	—	—	3	—	—	1
3	—	—	—	4	—	—	1	2	—	—	—	3	—	—	1
4	—	—	—	4	—	—	1	3	—	—	—	4	—	—	3
5	—	—	—	4	—	—	2	4	—	—	—	4	—	—	3
6	—	—	—	8	—	—	3	5	—	—	—	4	—	—	3
7	—	—	—	8	—	—	4	7	—	—	—	4	—	—	6
8	—	—	—	9	—	—	4	7	—	—	—	4	—	—	7

	1938					1939					1940				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
9 July	—	—	2	9	—	—	1	8	5	—	1	7	—	—	9
10	—	—	2	9	—	—	1	8	7	—	2	8	—	—	11
11	—	—	3	9	—	—	3	8	8	—	2	8	—	—	11
12	2	3	3	11	—	—	3	8	8	—	2	8	—	—	12
13	2	4	4	11	—	—	3	8	8	1	2	8	—	—	13
14	3	4	6	11	1	—	5	11	9	4	3	8	—	—	13
15	3	4	6	11	1	—	5	12	9	7	—	8	—	—	13
16	3	4	6	11	1	—	6	12	10	9	—	9	—	—	13
17	3	7	6	11	1	—	8	13	11	12	—	9	—	—	13
18	4	8	8	12	1	—	8	14	11	13	—	10	—	—	13
19	6	10	13	13	3	—	8	—	12	14	—	10	—	—	14
20	6	10	14	14	3	—	12	—	13	—	—	11	—	—	—
21	6	12	—	—	4	—	12	—	13	—	—	11	—	—	—
22	8	13	—	—	4	1	13	—	13	—	—	11	—	—	—
23	8	—	—	—	6	1	—	—	13	—	—	12	—	—	—
24	8	—	—	—	7	1	—	—	13	—	—	—	—	—	—
25	8	—	—	—	11	1	—	—	13	—	—	—	—	—	—
26	8	—	—	—	11	1	—	—	13	—	—	—	—	—	—
27	8	—	—	—	11	1	—	—	14	—	—	—	—	—	—
28	9	—	—	—	11	2	—	—	—	—	—	—	—	—	—
29	9	—	—	—	12	2	—	—	—	—	—	—	—	—	—
30	9	—	—	—	12	2	—	—	—	—	—	—	—	—	—
31	9	—	—	—	12	2	—	—	—	—	—	—	—	—	—
1 Aug.	9	—	—	—	13	2	—	—	—	—	—	—	—	—	—
2	9	—	—	—	14	3	—	—	—	—	—	—	—	—	—
3	10	—	—	—	—	3	—	—	—	—	—	—	—	—	—
4	—	—	—	—	—	5	—	—	—	—	—	—	—	—	—

Phleum pratense L.

Deaths. No further deaths have occurred on any of the soils.

General tone and habit. The sequence (best first) throughout the three years has been Potterne soil, clay, chalky clay, sand, calcareous sand. The difference between the last two was very marked. Compactness has been constant in exactly the reverse order. Cloning was most marked on the sands. Hummocking was most marked on Potterne soil and the sands.

Maximum height of flowering stems per ramet, in cm.

1938	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	26	26	25	25	26
Maximum	98	90	105	105	120
Minimum	68	60	68	75	98
Mean	84·5	77·5	96·3	87·9	112·0
Standard deviation	7·9	9·0	10·1	10·0	7·4

1939					
Number of ramets	26	26	25	25	26
Maximum	105	90	135	128	135
Minimum	90	68	90	113	113
Mean	94·8	81·0	116·8	116·1	128·3
Standard deviation	5·7	7·1	10·4	6·5	7·0

1940					
Number of ramets	26	26	25	25	26
Maximum	105	97	134	135	145
Minimum	74	68	95	102	117
Mean	90·8	79·8	119·2	117·1	126·6
Standard deviation	9·4	8·4	9·7	8·5	5·9

Number of flowering stems per ramet

1938	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	26	26	25	25	26
Maximum	52	11	104	48	117
Minimum	11	1	16	13	34
Mean	24·7	4·2	40·8	27·0	80·7
Standard deviation	11·3	2·2	18·4	14·0	24·3
Total per soil	640	109	1019	675	2098

1939	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	26	26	25	25	26
Maximum	79	20	104	83	150
Minimum	21	4	27	27	35
Mean	38·1	10·0	49·3	50·8	90·1
Standard deviation	14·9	4·1	17·0	16·4	31·1
Total per soil	990	260	1232	1269	2343

1940	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	26	26	25'	24	26
Maximum	93	32	122	114	204
Minimum	16	5	27	31	54
Mean	45·5	13·8	61·6	59·4	117·8
Standard deviation	18·3	6·1	23·2	20·7	51·6
Total per soil	1182	360	1541	1426	3064

Seedlings

	13. ii. 38	24. iv. 38	27. x. 38	5. ii. 39	10. iv. 39
Sand	None	Very numerous	Numerous	Numerous	Numerous
Calcareous sand	None	Numerous	Numerous	Numerous	Few
Clay	None	Numerous	Numerous	Few	Few
Chalky clay	None	Very numerous	Numerous	Few	Very few
Potterne soil	None	Very numerous	Few	Few	Numerous

	16. x. 39	19. iii. 40	16. ix. 40	17. xi. 40
Sand	Very few	Very few	Very few	Few
Calcareous sand	Very few	Numerous	Very few	Very few
Clay	Few	Very few	Very few	Very numerous
Chalky clay	Very few	Very few	Very few	Numerous
Potterne soil	Few	Very few	Very few	Numerous

First flowering

	1938 Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	1939 Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	1940 Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
22 June	—	—	—	—	—	—	—	—	—	—	26	9	17	22	5
23	—	—	—	—	—	—	—	—	—	—	—	9	17	22	5
24	—	—	—	—	—	—	—	—	—	—	—	9	17	22	5
25	—	—	—	—	—	—	—	—	—	—	—	24	25	25	25
26	—	—	—	—	—	—	—	—	—	—	—	24	—	—	25
27	—	—	—	—	—	—	—	—	—	—	—	24	—	—	25
28	—	—	—	—	—	—	—	—	—	—	—	24	—	—	25
29	—	—	—	—	—	—	—	—	—	—	—	26	—	—	26
30	—	—	—	—	—	—	—	5	1	—	—	—	—	—	—
1 July	—	—	—	—	—	—	—	5	1	—	—	—	—	—	—
2	—	—	—	—	—	16	4	10	13	—	—	—	—	—	—
3	—	—	—	—	—	16	4	11	13	—	—	—	—	—	—
4	—	—	—	—	—	26	20	24	25	18	—	—	—	—	—
5	—	—	—	—	—	—	25	25	—	26	—	—	—	—	—
6	—	—	—	—	—	—	25	—	—	—	—	—	—	—	—
7	2	8	4	3	—	—	25	—	—	—	—	—	—	—	—
8	26	22	21	25	7	—	25	—	—	—	—	—	—	—	—
9	—	22	21	—	8	—	25	—	—	—	—	—	—	—	—
10	—	22	21	—	8	—	26	—	—	—	—	—	—	—	—
11	—	22	25	—	25	—	—	—	—	—	—	—	—	—	—
12	—	26	—	—	26	—	—	—	—	—	—	—	—	—	—

Maximum florifery on all soils occurred on 14. vii. 38, 10. vii. 39, and 1. vii. 40. The florets open in the evening about 8 p.m. (double summer time).

Spring growth. Old leaves die in late autumn and new growth commences in February. Most early growth is shown on Potterne soil, then, in sequence, on chalky clay, clay, sand, calcareous sand.

Phleum nodosum L.

Deaths. No deaths have occurred on any of the plots.

General tone and habit. The sequence for tone (best first) has been maintained as Potterne soil, clays, sands, with some fluctuations between sand and calcareous sand and between clay and chalky clay respectively. All plants on all plots showed hummocky growth which was firmest on the sands. Early spring growth was evident on all plots by February and the final order, scored on 11. iii. 40, was (most first): Potterne soil, clays, and sands.

Seedlings. The clone remained self-sterile and no seedlings appeared.

Maximum height of flowering stems per ramet, in cm.

1939	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	26	26	26	26	26
Maximum	40	41	62	56	70
Minimum	13	19	40	27	43
Mean	30·8	27·7	52·3	41·4	58·4
Standard deviation	6·2	6·0	5·7	8·3	6·8
1940					
Number of ramets	21	22	26	26	26
Maximum	39	46	57	62	64
Minimum	6	6	36	39	38
Mean	33·0	29·5	46·6	53·7	50·4
Standard deviation	8·4	9·0	5·7	5·4	7·4

Number of flower stems per ramet

1938	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	26	26	26	26	26
Maximum	15	5	57	17	144
Minimum	1	0	4	1	10
Mean	5·8	1·1	26·4	9·2	42·2
Standard deviation	3·5	1·4	9·9	5·1	29·4
Total per soil	151	28	687	238	1098
1939					
Number of ramets	26	26	26	26	26
Maximum	73	49	234	132	494
Minimum	2	7	58	33	86
Mean	42·7	19·8	125·0	72·2	270·6
Standard deviation	17·6	10·0	40·1	25·1	114·7
Total per soil	1109	515	3249	1876	6936
1940					
Number of ramets	26	26	26	26	26
Maximum	11	25	109	150	110
Minimum	0	0	22	25	37
Mean	3·6	6·9	57·3	74·0	66·8
Standard deviation	2·8	6·5	24·2	26·6	25·5
Total per soil	94	179	1319	1923	1738

First flowering

	1938					1939					1940				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
7 July	—	—	—	—	—	—	—	—	—	—	—	—	2	1	—
9	—	—	—	—	—	—	—	—	—	—	—	—	4	1	—
14	—	—	—	—	—	—	—	—	—	—	—	—	15	8	5
15	—	—	—	—	—	—	—	—	—	—	—	—	16	8	6
17	—	—	—	—	—	—	—	—	—	—	—	1	20	11	7
18	—	—	—	—	—	—	—	—	—	—	—	1	21	11	7
19	—	—	—	—	—	—	—	—	—	—	—	1	22	12	7
20	—	—	—	—	—	—	—	—	—	—	—	1	23	19	7
21	—	—	—	—	—	—	—	—	—	—	—	2	23	20	7
22	—	—	—	—	—	—	—	3	1	—	—	2	23	21	7
23	—	—	—	—	—	—	—	4	1	—	—	4	25	24	13
24	—	—	—	—	—	—	—	12	1	3	—	4	26	25	13
25	—	—	—	—	—	—	—	12	1	3	—	5	—	25	13
26	—	—	1	—	—	—	—	17	5	7	—	5	—	25	13
27	—	—	3	—	—	—	—	19	6	11	2	7	—	25	18
28	—	—	4	—	—	—	—	19	6	12	2	7	—	25	18
29	—	—	7	—	—	—	—	22	8	12	3	9	—	26	21
30	—	—	7	—	—	—	—	22	8	12	3	9	—	—	21
31	—	—	10	—	—	—	—	23	11	13	3	9	—	—	21
1 Aug.	—	—	12	—	9	—	—	25	12	14	4	9	—	—	26
2	—	—	15	—	11	—	—	25	14	21	5	9	—	—	—
3	—	—	19	—	13	—	—	25	19	21	6	10	—	—	—
4	—	—	19	1	13	1	—	25	19	21	8	12	—	—	—
5	—	—	19	2	14	1	—	25	19	21	8	14	—	—	—
6	2	2	20	5	16	11	3	26	25	26	9	15	—	—	—
7	4	3	20	8	18	12	6	—	26	—	9	15	—	—	—
8	8	3	20	10	20	13	6	—	—	—	9	15	—	—	—
9	8	3	20	10	20	13	6	—	—	—	10	18	—	—	—
10	8	3	20	10	20	13	6	—	—	—	11	19	—	—	—
11	8	3	20	10	20	13	6	—	—	—	11	19	—	—	—
12	12	4	21	16	26	20	17	—	—	—	11	19	—	—	—
13	—	4	23	16	—	20	17	—	—	—	11	21	—	—	—
14	—	4	23	16	—	20	17	—	—	—	11	—	—	—	—
15	—	4	24	16	—	22	20	—	—	—	12	—	—	—	—
16	—	6	—	17	—	22	20	—	—	—	13	—	—	—	—
17	—	—	—	—	—	24	20	—	—	—	13	—	—	—	—
18	—	—	—	—	—	24	22	—	—	—	15	—	—	—	—
20	—	—	—	—	—	25	24	—	—	—	15	—	—	—	—
22	—	—	—	—	—	—	25	—	—	—	15	—	—	—	—
23	—	—	—	—	—	—	26	—	—	—	18	—	—	—	—
25	—	—	—	—	—	—	—	—	—	—	19	—	—	—	—

Maximum florifery. In 1938, florifery was so irregular that it was not possible to say when there was a maximum. In 1939, maximum florifery was on 12. viii. 39, and in 1940, on sands on 9. viii. 40 and on clays and Potterne soil on 1. viii. 40.

Fragaria vesca L.

This account deals only with the continuation of the redistribution experiments.

Deaths occurred as follows: 1938, Nos. 17, 49, 53, 57, 93, 141; 1939, Nos. 65, 77, 98; 1940, Nos. 12, 24, 51, 54, 61, 65, 144, 145.

Seedlings

	13. ii. 38	24. iv. 38	12. viii. 38	10. iv. 39	9. viii. 39
Sand	Very numerous	Very numerous	Numerous	Few	Very few
Calcareous sand	Few	Very numerous	Very few	Numerous	None
Clay	Numerous	Very few	Few	Very few	Very few
Chalky clay	Numerous	Very few	None	Very few	Very few
Potterne soil	Very numerous	Numerous	None	Numerous	Numerous

	16. x. 39	19. iii. 40	17. iv. 40	26. ix. 40
Sand	None	None	Very few	None
Calcareous sand	None	None	Very few	Very few
Clay	None	None	Very few	None
Chalky clay	None	None	Very numerous	Very few
Potterne soil	Very few	None	Very numerous	Very few

Cloning of whole plant. The general tone was scored (best first) as follows:

11. iv. 38	12. viii. 38	10. iv. 39	9. viii. 39	9. v. 40	15. ix. 40
Calcareous sand	Potterne soil	Chalky clay,	Potterne soil	Potterne soil	Chalky clay
Chalky clay	Chalky clay	Clay	Chalky clay	Chalky clay	Clay
Potterne soil	Calcareous sand	Potterne soil	Clay	Clay	Potterne soil
Clay	Clay	Calcareous sand	Calcareous sand	Calcareous sand	Calcareous sand
Sand	Sand	Sand	Sand	Sand	Sand

		Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Runners:	1938	4	30	48	41	34
	1939	3	26	18	58	41
	1940	6	10	38	21	32
Stem heights	1938	10	15	13	17	11
in cm.	1939	6	9	14	18	16
(fruiting):	1940	8·5	7	13	20	16
First flowers:	1938	5. v.	6. v.	9. v.	28. iv.	5. v.
	1939	11. v.	10. v.	8. v.	4. v.	10. v.
	1940	14. v.	7. v.	7. v.	5. v.	5. v.
First fruits:	1938	6. vii.	None	24. vi.	27. vi.	24. vi.
	1940	15. vi.	None	14. vi.	12. vi.	11. vi.

General tone, for ramets on every soil taken as one sample. The sequence (best first) for the three years was Potterne soil, clay, chalky clay, calcareous sand, sand, except for a slight fluctuation in the order of clay and chalky clay.

General tone of groups. This was scored every year, but it is necessary here to give only the values for the final scoring on 15. ix. 40. As in the last report marks are awarded to 5 ramets. These marks are relative only for the groups on the soil on which the ramets grew for about four and a half years. The value 5 is best tone, 4 not so good, and so on.

Now on From ...	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Sand	5	4	2	3	1
Calcareous sand	3	5	2	4	1
Clay	4	3	1	5	2
Chalky clay	3	4	1	5	2
Potterne soil	4	2	1	5	3
Totals	19	18	7	22	9

The sequence of totals is the same as it was in 1936 to 1937, except that sand and calcareous sand have changed places.

Runners. Total number of runners per transferred ramet (i.e. group of five new ramets), (*a*) for 1938, (*b*) for 1939, (*c*) for 1940:

Now on From ...	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Sand	(*a*) 114	(*a*) 87	(*a*) 125	(*a*) 181	(*a*) 49
	(*b*) 84	(*b*) 86	(*b*) 90	(*b*) 117	(*b*) 53
	(*c*) 64	(*c*) 71	(*c*) 32	(*c*) 56	(*c*) 38
Calcareous sand	(*a*) 201	(*a*) 206	(*a*) 76	(*a*) 218	(*a*) 125
	(*b*) 295	(*b*) 281	(*b*) 146	(*b*) 355	(*b*) 182
	(*c*) 178	(*c*) 238	(*c*) 113	(*c*) 218	(*c*) 114
Clay	(*a*) 191	(*a*) 225	(*a*) 51	(*a*) 263	(*a*) 130
	(*b*) 331	(*b*) 323	(*b*) 91	(*b*) 423	(*b*) 191
	(*c*) 296	(*c*) 244	(*c*) 83	(*c*) 311	(*c*) 121
Chalky clay	(*a*) 143	(*a*) 162	(*a*) 104	(*a*) 277	(*a*) 321
	(*b*) 223	(*b*) 262	(*b*) 191	(*b*) 334	(*b*) 322
	(*c*) 98	(*c*) 88	(*c*) 52	(*c*) 186	(*c*) 95
Potterne soil	(*a*) 136	(*a*) 142	(*a*) 136	(*a*) 324	(*a*) 143
	(*b*) 286	(*b*) 267	(*b*) 145	(*b*) 427	(*b*) 204
	(*c*) 174	(*c*) 175	(*c*) 72	(*c*) 240	(*c*) 208

Mean stem heights, in cm., for groups of five new ramets, (a) for 1938, (b) for 1939, (c) for 1940:

Now on / From ...		Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Sand	(a)	13·5	8·3	15·4	17·6	10·6
	(b)	13·2	7·6	13·2	13·0	10·0
	(c)	11·6	9·4	10·5	10·4	8·3
Calcareous sand	(a)	20·2	16·0	13·8	22·2	15·3
	(b)	23·0	23·2	14·4	18·8	21·0
	(c)	17·8	18·4	15·6	17·6	17·5
Clay	(a)	24·8	24·4	13·3	24·0	15·6
	(b)	23·8	26·3	12·3	28·8	20·6
	(c)	25·3	16·7	12·1	25·1	16·8
Chalky clay	(a)	22·4	17·2	20·4	21·2	22·0
	(b)	21·2	17·2	18·8	26·0	19·0
	(c)	20·6	18·5	19·3	21·0	20·3
Potterne soil	(a)	24·4	18·8	15·0	27·4	21·3
	(b)	21·0	16·8	13·0	20·4	15·4
	(c)	26·0	19·0	13·7	25·3	22·8

Primary flowering and primary fruiting. The scheme below gives the mean first flowering date in May for the groups of five new ramets, (a) for 1938, (b) for 1939, and (c) for 1940, and the mean first ripening of fruit for June, (d) for 1938, and (e) for 1940. The few minus values in (a) and (b) refer to dates in April calculating backwards from the last day of that month.

Now on / From ...		Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Sand	(a)	7·0	3·8	5·0	5·8	8·6
	(b)	7·2	8·2	7·2	8·0	9·8
	(c)	8·8	9·2	9·5	8·5	9·8
	(d)	25·0	—	24·7	31·3	34·5
	(e)	15·0	14·0	11·3	12·3	15·0
Calcareous sand	(a)	−2·2	−4·0	0·0	3·0	−2·5
	(b)	−2·2	−3·8	−1·6	1·6	6·3
	(c)	4·4	4·6	8·0	4·4	8·3
	(d)	22·2	23·0	26·2	22·6	30·3
	(e)	12·0	13·0	16·0	13·6	14·8
Clay	(a)	−1·0	−1·0	−1·3	0·6	6·7
	(b)	−0·3	5·5	6·8	3·8	7·6
	(c)	4·8	6·3	28·0	7·4	6·0
	(d)	24·8	23·6	28·0	24·2	27·0
	(e)	10·5	11·7	15·0	12·4	14·6
Chalky clay	(a)	−3·4	3·8	1·6	−3·1	0·8
	(b)	0·8	4·2	−1·0	3·8	4·8
	(c)	9·2	10·8	7·8	6·3	5·5
	(d)	24·6	26·5	26·4	23·2	29·0
	(e)	14·3	14·4	12·3	11·5	11·8
Potterne soil	(a)	−6·0	0·8	4·2	−2·6	−6·2
	(b)	4·2	9·4	7·5	8·8	5·6
	(c)	4·2	6·0	15·0	6·6	6·0
	(d)	21·0	21·4	26·3	22·4	21·5
	(e)	11·0	12·0	11·0	11·8	10·5

Chlorosis was marked in most of the plants on chalky clay during 1938 and 1939 but became less marked in 1940.

Spring growth. Plants tended to be evergreen, though outermost leaves browned off in winter and still more after spring shooting. Spring growth started again in February or March and was slowest on the sands.

Heaping up of stones and soil around plants was most marked on calcareous sand, then, in descending order, on chalky clay, sand, Potterne soil, clay.

Adventitious roots continue to arise from stem bases as these rot upwards on all soils.

Flowering. Between 2. v. 39 and 7. v. 39 a considerable number of flower buds were damaged by frost, particularly on chalky clay. Much secondary flowering occurred on all plots, least on sand.

Solanum dulcamara L. var. marinum Bab.

Description of Transplant stock, 13. viii. 38, when in flower and (mostly) with young (green) and a few mature fruits.

Primary branches of ramet prostrate, up to 9·5 dm. long; secondary branches spreading and subprostrate or ascending towards the ends, up to 2·6 dm. above the soil surface, all branches flowering. *Branches* with about five obtuse angles, flexuose in younger parts, subglabrous but with some scattered adpressed to spreading white hairs of different lengths, and microscopic adpressed curved glandular hairs on younger parts, suffused in varying degrees with dark anthocyanin, numerous stomata in younger and corky lenticels in lower parts. *Leaves* very varied in shape and lobing, in general outline ovate to broadly ovate, apex acute to subacuminate, base more or less cordate, lower leaves with lamina up to 7·5 cm. long and 5·9 cm. broad, upper leaves average 4 cm. long and 2·3 cm. broad, entire up to deeply 1–4-lobed below the middle, well marked midrib raised on both upper and lower surfaces with lateral veins arising mostly at a broad angle, hairs of short and medium length and a few gland-tipped on veins and near margins, in some leaves fewer hairs on lower than on upper surface; petiole up to 2·7 cm. long, with indumentum as for stems. *Inflorescences* 4–21-flowered; peduncles up to 3·3 cm. long with few spreading to adpressed hairs and a few glands; pedicels up to 9 mm. long, glabrous. *Calyx* glabrous or (in young state) with a few hairs and glands, lobes (at anthesis) nearly half-circular, 1·25 mm. long, 1·5 mm. broad. *Corolla* 2 cm. diam., lobes narrowly lanceolate, 9 mm. long, 3 mm. broad, colour 'Nigrosin Violet' (Ridgway, *Color Standards*, Pl. XXV), with two green nectaries at the base of each lobe, with very short hairs on lower surface and near margins. *Berries* ellipsoid, 11 mm. long, 9 mm. diam., colour 'Brazil Red' (Ridgway, *Color Standards*, Pl. I).

The ramets used for the experiments were obtained from cuttings of tertiary branches from an F_1 plant (No. 9) of stock-plant 12. This stock-plant was collected on shingle at Dungeness, Kent, 17. ix. 33, by H. W. B. Barlow. The plant was selfed under control and gave a uniform family of forty-four plants. One of these (No. 9) was cloned on 17. vii. 37 and the ramets re-cloned on 25. viii. 38. They were rooted in Potterne soil and transplanted to the plots on 15. iv. 39. These final ramets were erect when transplanted. The plant No. 9 was also selfed under control and a family of fifty plants, all uniform, was raised.

Deaths. No deaths occurred on any of the plots.

General tone (best first) was recorded as follows:

26. vi. 39	8. viii. 39	17. vii. 40 and 20. ix. 40
Potterne soil	Clay	Clay
Clay	Potterne soil	Chalky clay
Chalky clay	Chalky clay	Potterne soil
Calcareous sand	Calcareous sand	Calcareous sand
Sand	Sand	Sand

Rooting at nodes. The only plants to produce adventitious roots from aerial nodes, up to 19. xi. 40, were all on clay: No. 52 (one root), No. 54 (three roots from one node), and

No. 55 (one root). Roots from rhizomes appeared at the surface on clay, chalky clay, and Potterne soil, but not on the sands (11. iii. 40).

Winter die-back of shoots. After frost, shoots died back several cm. on sand, calcareous sand, and Potterne soil (11. iii. 40). There was no apparent die-back on clay or chalky clay.

Branching habit. All the ramets, when transplanted, were erect tertiary branches and were transplanted erect. The gradual assumption of the prostrate branch habit characteristic of the variety is shown by the following selected scorings:

17. v. 39. Slight inclination of branches noted on all plots.

26. vi. 39. Branches beginning to bend over on all plots.

8. viii. 39. Sand: little growth, no branches prostrate. Calcareous sand: more growth, branches becoming horizontal, but some erect ones still present. Clay: very considerable growth and masses of prostrate branches produced. The ramets are very like coastal populations growing *in situ*. Chalky clay: very considerable growth, horizontal and erect branches present. Potterne soil: very considerable growth, prostrate stems have developed, but there are still some erect branches.

2. x. 39. Sand: little growth, branches inclining but none prostrate. Calcareous sand: more growth, most branches horizontal but a few arched and prostrate branches present. Clay: very considerable growth with arched and prostrate branches. Potterne soil: very considerable growth, branches mostly horizontal but some prostrate.

20. ix. 40. Sand: only one plant had made significant growth and this now showed prostrate branches. Calcareous sand: more, but not lush, growth, all ramets with some prostrate branches. Clay: very lush growth, all ramets with arched and prostrate branches. Chalky clay: very lush growth, all ramets with arched and prostrate branches. Potterne soil: somewhat lush but rather later growth, with prostrate and often arched branches.

		Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
			Longest shoot per ramet			
4. x. 39	Max. in dm.	2·25	4·05	10·80	9·80	10·40
	Min. ,,	1·18	2·90	9·70	5·00	4·10
	Mean ,,	1·56	3·43	10·38	6·82	6·58
12. ix. 40	Max. ,,	6·90	7·50	14·00	13·30	14·00
	Min. ,,	0·40	3·80	13·00	8·20	5·30
	Mean ,,	2·47	5·38	13·50	10·25	8·40
			Total spread per ramet			
4. x. 39	Max. in dm.	2·00	6·65	16·84	13·60	13·40
	Min. ,,	0·87	3·20	16·00	9·00	7·50
	Mean ,,	1·34	4·85	16·37	10·77	10·40
12. ix. 40	Max. ,,	8·70	10·90	23·40	23·00	20·60
	Min. ,,	0·00	6·90	21·50	14·60	9·80
	Mean ,,	2·27	8·90	22·50	18·56	16·06
			Height above soil level			
4. x. 39	Max. in dm.	1·25	2·20	2·36	2·47	2·90
	Min. ,,	0·70	1·60	1·60	1·60	2·30
	Mean ,,	1·00	2·00	1·99	2·02	2·51
12. ix. 40	Max. ,,	1·70	3·10	3·00	3·55	3·65
	Min. ,,	0·40	2·20	2·20	2·40	1·90
	Mean ,,	1·26	2·50	2·56	2·90	2·56

Flower buds showed before anthesis on 10. iv. 40 in the order (most advanced first): clay, chalky clay, calcareous sand, Potterne soil, sand.

First flowering

| | 1939 | | | | | 1940 | | | | |
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
19 May	—	—	—	—	—	—	—	1	—	—
20	—	—	—	—	—	—	—	3	—	—
21	—	—	—	—	—	—	1	4	3	—
22	—	—	—	—	—	—	1	4	4	1
23	—	—	—	—	—	—	1	5	4	1
24	—	—	—	—	—	—	1	—	5	1
25	—	—	—	—	—	—	2	—	—	3
26	—	—	—	—	—	—	2	—	—	3
27	—	—	—	—	—	—	2	—	—	3
28	—	—	—	—	—	—	3	—	—	4
29	1	—	—	—	—	—	3	—	—	4
30	1	—	—	—	—	—	5	—	—	4
31	1	1	1	1	—	—	—	—	—	4
1 June	1	2	1	1	—	—	—	—	—	4
2	1	3	2	5	—	—	—	—	—	4
3	3	5	4	—	3	1	—	—	—	4
4	3	—	5	—	4	1	—	—	—	5
5	4	—	—	—	4	2	—	—	—	—
6	5	—	—	—	5	2	—	—	—	—
7	—	—	—	—	—	2	—	—	—	—
8	—	—	—	—	—	2	—	—	—	—
9	—	—	—	—	—	2	—	—	—	—
10	—	—	—	—	—	3	—	—	—	—
11	—	—	—	—	—	4	—	—	—	—

Maximum florifery occurred on all plots on 5. vi. 40. On the same date the degree of florifery (most floriferous first) was in the order: clay, chalky clay, Potterne soil, calcareous sand, sand.

First fruiting

| | 1939 | | | | | 1940 | | | | |
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
5 July	—	—	—	—	—	—	—	1	—	—
10	—	—	—	—	—	—	—	4	2	—
11	—	—	—	—	—	—	1	4	2	—
12	—	—	—	—	—	—	1	5	4	—
13	—	—	—	—	—	—	1	—	5	—
14	—	—	—	—	—	—	2	—	—	—
18	—	—	—	—	—	—	3	—	—	1
19	—	—	—	—	—	—	4	—	—	1
20	—	—	—	—	—	—	5	—	—	3
23	—	—	—	—	—	—	—	—	—	4
24	—	—	—	—	—	1	—	—	—	4
29	—	—	1	—	1	—	—	—	—	5
3 Aug.	—	—	2	—	2	—	—	—	—	—
4	—	—	3	1	3	—	—	—	—	—
8	—	1	3	2	4	—	—	—	—	—
9	2	1	4	3	5	—	—	—	—	—
10	2	2	4	3	—	—	—	—	—	—
11	3	3	4	4	—	—	—	—	—	—
12	3	3	4	5	—	—	—	—	—	—
13	3	4	4	—	—	—	—	—	—	—
14	3	—	5	—	—	—	—	—	—	—
17	4	—	—	—	—	—	—	—	—	—

Size of berries. The length and diameter of a random sample of 50 berries from every soil was measured (except from sand on which insufficient berries to reach this figure were produced). Here it suffices to give maximum and minimum figures in mm. for the two years.

	1939		1940	
	Max.	Min.	Max.	Min.
Sand	9·5 × 7·0	9·0 × 7·0	11·0 × 9·0	10·0 × 8·5
Calcareous sand	10·5 × 9·0	8·0 × 7·5	10·0 × 9·0	8·5 × 7·0
Clay	12·0 × 10·0	10·0 × 9·0	10·8 × 8·5	9·0 × 8·0
Chalky clay	11·0 × 10·5	10·0 × 9·0	11·0 × 9·5	9·0 × 8·0
Potterne soil	11·0 × 9·5	9·0 × 8·0	11·0 × 8·5	9·0 × 7·5

Number of berries produced on the most fructiferous infructescence on every ramet:

	1939			1940		
	Max.	Min.	Mean	Max.	Min.	Mean
Sand	3	1	1·8	18	0	3·8
Calcareous sand	14	7	10·8	12	6	10·4
Clay	19	16	17·6	13	11	12·0
Chalky clay	15	9	12·8	21	10	14·4
Potterne soil	18	16	17·2	14	7	11·2

Seedlings. These first appeared on 17. iv. 40. Germination is continuous throughout the summer. The seedlings on the plots tend to germinate in clumps, corresponding to the many-seeded berries. One clump on Potterne soil had 34 seedlings.

	17. iv. 40	20. ix. 40
Sand	None	None
Calcareous sand	Very few	Numerous
Clay	Very few	Numerous
Chalky clay	None	Very numerous
Potterne soil	Very numerous	Numerous

Berries remaining on plants. Plants retained their berries till the end of December, after the leaves had all dropped. On the clays and Potterne soil many berries were ruptured on the plants and others fell on the soil around.

SUMMARY AND CONCLUSIONS

1. Figures for rainfall, temperature, and humidity are given for 1938, 1939, and the first nine months of 1940.

Attention may be called to the figures for relative humidity. These have been extracted from the continuous graphs which are often extremely regular in their nocturnal rise and diurnal fall. It is suggested that this factor, which is only partially correlated in a direct manner with temperature variations, deserves more intensive study in its influence on plant behaviour than it has yet received.

2. The results of periodic records on the species investigated during the three years are embodied in this report. The chief facts that have emerged and their relationships with earlier results are:

Centaurea nemoralis. This species has been on the plots continuously for the 13 years of the experiments and has proved a persistent perennial on all the soils. For the whole period the ratio of total ramets used to total deaths is 5·4 : 1. No deaths have occurred on sand or calcareous sand. No morphological differences between the ramets on the different soils have appeared. The habit differences, due either to soil or climate, between ramets (of one and the same clone) at Kew (stems widely ascending) and at Potterne (stems erect) have been maintained for the 13 years. It is extremely interesting that this species has shown the best results, for general tone and most of the characters scored separately, on sand, second best results on calcareous sand, and the worst on Potterne

soil. The significance is all the more striking when we examine the tables, at the end of this summary, in which it is made clear that sand is the most unfavourable of the Transplant soils for a majority of the species tested. The total numbers of flowering stems show fluctuations for the three years but, when compared with results in earlier years and correlated with the meteorological record, these fluctuations are clearly seen to be due to annual weather conditions, especially to early summer rainfall and temperature, and not to any progressive soil exhaustion.

Silene maritima (narrow-leaved variety). No morphological changes were observable in ramets on any of the soils, except that leaves of those on sand were, ⌐n the whole, slightly smaller than those of ramets on other soils. Other striking characters of the clone—deep anthocyanin, narrow leaves, narrow calyx, and essential femaleness—remained constant on all soils. Differential death rates were remarkable. Only three ramets out of 26 remained alive on sand for the $2\frac{2}{3}$ years of the experiment with this plant. On the other soils there were no deaths, 26 ramets surviving on every one. Features of the root system vary on the different soils and are comparable to those recorded earlier for typical *Silene maritima*.

Plantago major (large variety). More deaths have been recorded, particularly on sand. The general tone has changed slightly from that of earlier scorings and finally became stabilized with chalky clay best and sand worst. The scorings for individual characters mostly agreed with this evaluation.

It is of some importance to compare the results obtained with this large variety of *Plantago major*, for the years 1936 to 1940, with those obtained with the small variety for 1928 to 1934. Breeding and other controlled experiments showed that the two stocks were genetically distinct. On the Transplant soils they behaved in one sense very similarly, in another in an almost reversed manner. In both varieties, though with some fluctuations, the plants did best on clays and Potterne soil, worse on calcareous sand, and worst on sand. The small variety became larger on the clays and Potterne soil, the large variety became smaller on the sands. The death-rates were particularly high on sand for both varieties and on chalky clay and Potterne soil for the small variety as the following table shows:

	Alive Small variety (after 6 years)	Alive Large variety (after 5 years)
Sand	8 out of 26	3 out of 14
Calcareous sand	8 ,, 26	11 ,, 14
Clay	22 ,, 26	10 ,, 14
Chalky clay	0 ,, 26	14 ,, 14
Potterne soil	3 ,, 26	14 ,, 14

In spite of the fact that there was some tendency for the gross morphological characters to become similar in the two varieties when grown on any one soil, the differences between the two varieties were never obliterated and there were different physiological reactions as indicated by death-rates, in regard to drought resistance and disease and pest attack, and rate of seedling development.

Phleum pratense has survived without further deaths on any soil. The general tone has been constant for the sequence: Potterne soil (best), clay, chalky clay, sand, calcareous sand. Detailed scorings of characters showed the same sequence, with some fluctuations between the clays. Actual figures show variations within the range of those for recent

years with no fixed or regularly continuing increases or decreases. These facts suggest that the differential reactions to the soils have reached a degree of equilibrium without, as yet, there being any sign of soil exhaustion.

Phleum nodosum has survived without any deaths on any of the soils during the nine years the species has been used in the Transplant experiments. The general tone has kept constant for the sequence (best first): Potterne soil, clay, chalky clay, sand, calcareous sand. Actual figures show variations within the general range for recent years with no fixed or regularly continuing increases or decreases. The summer drought of 1940 reduced the numbers of flowering stems considerably. This contrasts with the weather effects on *P. pratense*.

The five years' additional experience with the two timothy grasses since that recorded in our note on their taxonomy (*J. Ecol.* **25**, 206 footnote, 1937) confirms our conclusion that they must be regarded as belonging to distinct taxonomic species, whatever their origin and cytogenetic relationships. The various characters of size, habit, and structural details we have studied have remained different on the five soils of the Transplant experiments. There have been no changes in these characters from those of one species towards those of the other. On the whole, reactions to edaphic factors have been parallel in the two species but reactions to seasonal weather have sometimes been markedly different. The *Phleum nodosum* clone has remained self-sterile. Readers interested in the question of the relationship of *P. pratense* and *P. nodosum* may be referred to a paper by H. Nordenskiöld, 'Cytological studies in triploid *Phleum*', in *Bot. Notiser*, 1941, pp. 12–32. The question of sterility is discussed by Jenkin, 'Fertility in plants of the genus *Phleum*', in *Bull. Univ. Coll. Wales, Welsh Plant Breed. Sta.*, Series H, no. 12, 148–59, 1931.

Fragaria vesca. The present interest of this species on the Transplant soils centres in the recloned and redistributed groups, everyone of five ramets. These represent clones previously grown on every soil redistributed to every soil. For groups of ramets from different soils the results recorded show that those from chalky clay gave the best results, followed, apart from a few and usually insignificant fluctuations, by those from calcareous sand or sand and Potterne soil or clay (worst). It would appear that the calcium carbonate in some way acts as a favourable stimulus for growth, the influence being determinable for at least 5 years.

Solanum dulcamara var. *marinum* was only in position on the Transplant soil for 2 years. With other species we know that different reactions can become obvious on different soils within that period. It is, therefore, of interest to note that, wherever there was sufficient elongation the characteristic prostrate habit of growth appeared in the branches of ramets derived by repeated cloning from one original stock plant. The habit character of the variety has been shown to be genetic and also constant (not plastic) under the different plot conditions of the Transplant experiments. General tone and numerically determined characters of growth tended to become stable on the different soils in the following sequence (best first): clay, chalky clay, Potterne soil, calcareous sand, sand. The natural wild habitat of the variety is the shingle beach. It would appear that its occurrence on more or less stabilized shingle is not due to its better growth on such a substratum but to other factors, such as absence of severe competition from other plants, connected in turn with the ability of the variety to withstand sea winds, strong insolation, and even some sea spray.

3. Moss growth and slug attack were not pronounced during the three years but there was some spread of *Cladonia*.

4. Primary flowering has again been carefully recorded. *Centaurea nemoralis* increased its earliness of first flower development throughout the three years and was very early indeed in 1940. First flowering for *Plantago major* was particularly early in 1940 on clay and chalky clay. First flowering was early and quickly completed on all soils for *Phleum pratense* in 1940, but though on the whole that for *P. nodosum* was earlier in 1940 than for the two previous years it was longer drawn out and latest on calcareous sand and sand. The figures for first flowering (and for first fruiting) are given for *Fragaria vesca* but no generalization has emerged from their study. In *Solanum dulcamara* var. *marinum* first flowering and first fruiting was earlier in 1940 than in 1939, except for the rather extended first flowering on sand. It would appear that, in general, first flowering depends more on seasonal weather than on soils, but is modified by the latter.

5. In *J. Ecol.* **26**, 380–9, 1938, a summary of the results of the Transplant experiments was given for the 10 years, 1928–37. The present report is the final one. In conclusion, it may be useful to re-emphasize how very different have been the reactions of the species used to the edaphic conditions of the five plots. The following table gives the plants which showed maximum growth, vigour, and (usually) flowering and fruiting on the five soils and those that showed a minimum for such development. In preparing this table and the next the later scorings have been given a higher value than the earlier scorings, if there were differences. In terms of 'general tone' and other scorings one species 'did best' and another 'did worst' on every soil.

	Best	Worst
Sand	*Centaurea nemoralis*	*Silene maritima* (narrow-leaved variety) *Plantago major* (large variety) *P. major* (small variety) *Fragaria vesca* *Solanum dulcamara* var. *marinum* *Silene vulgaris* *Anthyllis vulneraria*
Calcareous sand	*Silene maritima*	*Phleum pratense* *P. nodosum*
Clay	*Solanum dulcamara* var. *marinum*	—
Chalky clay	*Silene maritima* (narrow-leaved variety) *Plantago major* (large variety) *Silene vulgaris*	—
Potterne soil	*Phleum pratense* *P. nodosum* *Fragaria vesca* *Anthyllis vulneraria* *Plantago major* (small variety)	*Centaurea nemoralis* *Silene maritima*

In the second tabulation (below) there is a summation for soils. A species 'doing best' on a soil gives the value 5 to that soil, 'doing second best' gives 4, and so on, down to 1 for the soil on which it 'does worst'. These figures are fairly accurate as relative evaluations since they are accorded on the basis of general tone and of scorings for detailed characters.

The summated result is:

Clay	40
Chalky clay	40
Potterne soil	39
Calcareous sand	28
Sand	20

PLANT LIFE IN KONGSFJORD, WEST SPITSBERGEN

By NICHOLAS POLUNIN, *Department of Botany, Oxford*

(*With Plates 6–9 and one Figure in the Text*)

1. INTRODUCTION

No account of the vegetation of the Kongsfjord region of Spitsbergen has so far been published, or at least none was available in 1940 when Norway came under enemy occupation. Nor is the general cryptogam or even the phanerogam flora at all well known. Kongsfjord, *ca.* 79° N. (see Fig. 1), runs in obliquely east-south-east for about 30 km. from the Arctic Ocean coast and forms a convenient regional entity for descrip-
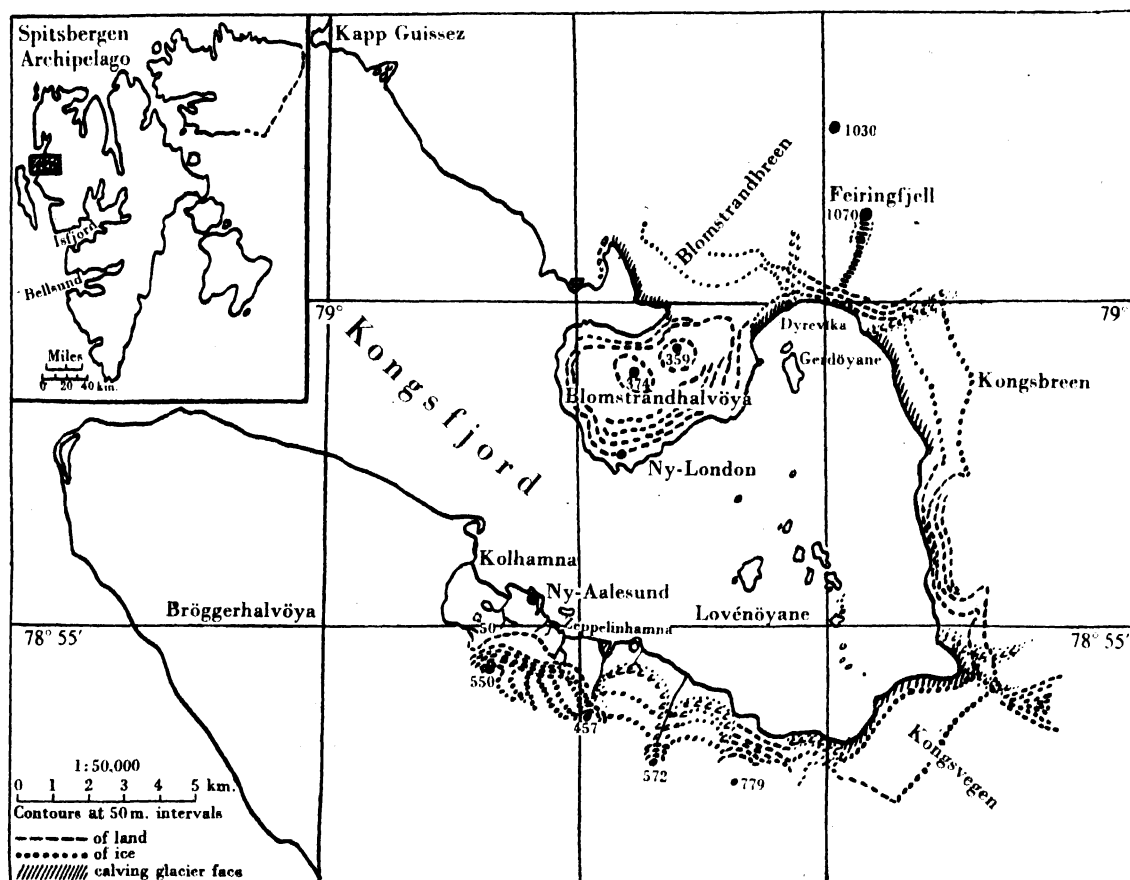
Fig. 1. Sketch-map of Kongsfjord (King's Bay), comprising area shaded in inset maplet (upper left-hand corner).

tion. It is interesting also in having a disused coal-mine, radio station, airship hangar, and 'post office'—all the farthest north in the world unless it may be for newer Russian ones, e.g. on Franz Josef Land. It was the place from which the dirigible 'Norge' made its historic flight to the North Pole in May 1926. Kongsfjord also supported for a time the farthest north cow in the world, and a piggery with sixty pigs. Moreover, during the years immediately preceding the present world war it came further into prominence

as the farthest north point of call—at least to land—of many of the pleasure cruises to the Arctic which were then becoming so popular. Almost every summer during the middle 1930's several great liners, filled with pleasure seekers who went there and proceeded even farther north in perfect luxury, visited Kongsfjord for a few hours or occasionally a day or two. Not since an earlier century when mariners of several nations fought all together for whaling 'rights' can any part of the Spitsbergen Archipelago well have resounded to such rowdy throngs as did Kongsfjord on those occasions in the pre-war years! To botanists who may have accompanied these cruises, and to others who may go there in the future, I offer the following account prepared around notes which I made during the summer of 1933 while on a Norwegian sealing and white-whaling expedition with that fine arctic pilot Captain Svenson of Tromsø. Some such account would appear particularly appropriate in this place and at this time, because the *Journal of Ecology* has long been noteworthy for its accounts of the vegetation of other parts of the Spitsbergen Archipelago (see references on pages 107 and 108), and because it seems desirable to bridge the gap between these former papers and those we may hope for in the better years to come.

The present account is of necessity far from complete, because although two visits were paid to Kongsfjord, one of them—on 27 July—was only for a single day, while the other—from 2 to 7 August—was for the purpose of resting and repairing our ship after a bad storm farther north. Nevertheless, by working at night as well as during the day, in a manner that is fortunately easy in such high-arctic lands, I was able to accomplish a fair amount of botanical field work. This was primarily directed, in the absence of sufficient time to do more than a fraction of what I would have wished, towards analysing the evident similarities between the vegetation and flora of exposed limestone areas with the vegetation and flora on the similarly exposed limestone surface of Akpatok Island (Polunin, 1934, 1935), situated nearly 19° of latitude farther south and more than 3200 km. (2000 miles) distant on the other side of the Atlantic.

It may be said at the outset that the vegetation of Kongsfjord is like that of all other areas in Spitsbergen in being always dwarf, no plants rising to a height of much more than 50 cm., while the general vegetation is less than half this maximum. Moreover, it is usually sparse and open; only occasionally in very localized areas where conditions of shelter, water supply, or available food substances are especially favourable, may it be closed and matted. Most of the area that is not covered by ice or mountains (whose upland regions were not examined around Kongsfjord but which probably almost everywhere support still poorer vegetation, as in the Bellsund region farther south) is occupied by *fjellmark*—stony desert (current Norw. 'mountain ground'), consisting of rock fragments of all sizes including much finer soil, the result largely of severe frost weathering. On this grows a greater or usually lesser abundance of the hardier plant species, generally in sparsely open formation. Here frost comminution and solifluction, and the various other agents of surface denudation which are so active in the Arctic, tend to give habitats which are occupied only by chance colonists, with the result that the micro-communities may be almost as much mixed as the plants themselves, the vegetation as a whole appearing to consist of an intricate assemblage of plants varying from place to place and with no particular dominant. This aspect has been stressed by Wager (1938), whose observations on the high death-rate of seedlings in fjellmark areas of East Greenland are most interesting even if Dobbs (1939) was unable to confirm them for Spitsbergen in

the summer of 1936 and although Wager's suggested explanation has been pertinently criticized by Russell (1940). Generally, however, one species is more or less dominant; but only in areas where conditions are particularly favourable can any one species or even life-form be so successful as to oust all competitors and cover the ground.

This paper describes examples of the main plant communities encountered in Kongsfjord and compares them cursorily with those of some other parts of Spitsbergen. The phanerogam and pteridophyte flora was collected as far as possible. The short lists of bryophytes and lichens which are given at the end of the paper merely comprise those species of these groups which were collected for the purpose of supplementing ecological lists or because they were especially abundant or conspicuous. Apart from the few Algae mentioned, no other cryptogams were identified among those of my collections from this place which reached England; however, a few of the more conspicuous Fungi occurring in one spot have recently been reported by Dobbs (1942).

2. Climate and other conditions affecting plant growth

As has already been pointed out by Summerhayes & Elton (1928), the local variations in the plant communities of Spitsbergen are generally to be related to the interaction of four independent environmental factors, viz. climate, underlying rock, water supply, and manuring by sea birds. To these should probably be added factors introduced by ice and snow, viz. the results of persistent phasic change and the period that had elapsed since deglaciation (especially short near some present-day glaciers), and the time of melting of the snow each year (this is especially late in areas where drifting is deep, with a corresponding reduction of the growing season). Climate is always the primary factor determining which of the major vegetation belts of the world a region falls into; but in Spitsbergen the local climatic and other conditions vary so greatly according to exposure (which itself is largely determined by local topography), that the vegetation may even vary drastically from spot to spot in the same general locality—often from one square metre to the next, as in the hilly areas around Ny-London (see below). It thus seems desirable, for a fuller understanding and to get a truer conception of the environmental conditions, to name topography before all the other factors. These main conditions affecting the vegetation will now be considered in somewhat greater detail, with special reference to Kongsfjord.

(a) Topography

Spitsbergen, almost everywhere a mountainous country, is especially so around Kongsfjord (see Pl. 6, phot. 1, in background). The slopes in many places rise steep and almost straight to the pointed peaks which give the land its name and which hereabouts often exceed 1000 m. in height. Sometimes the lower slopes start as screes or rough broken cliffs almost or quite at the edge of the sea, but generally in the Kongsfjord region they only commence to rise steeply behind a more gently sloping coastal outwash plain a kilometre or so wide, and dissected by glaciers which in some cases come right down to the sea (Pl. 6, phot. 1, in middle distance). These plains support most of the vegetation of the area, and it is mainly with them that we shall be concerned.

(b) Climate

The local climate is in these regions largely a function of exposure, which is itself dependent upon topography. However, in general terms it may be said that for a land
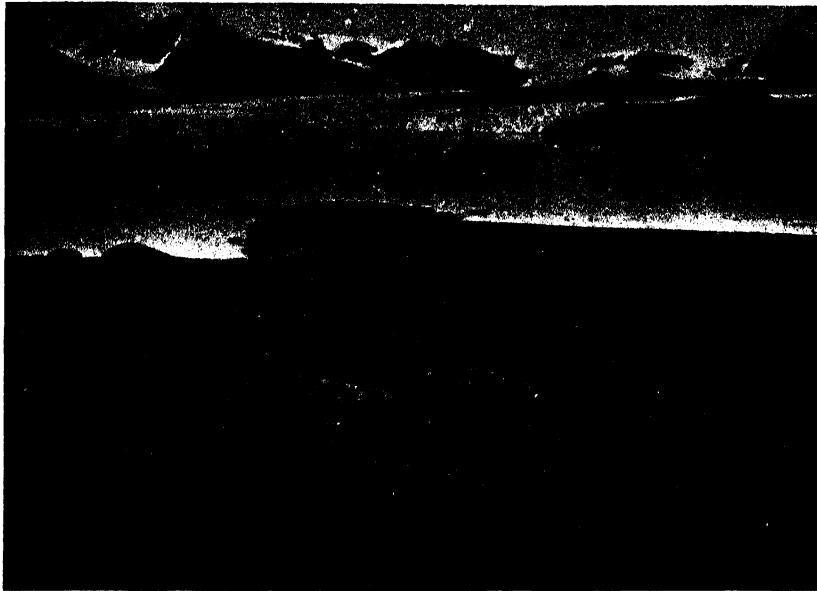
Phot. 1. Typically rugged country near the head of Kongsfjord, with a large glacier discharging into the sea (pp. 84, 90). Taken from a 'bird' island (pp. 86, 98), the manured foreground supporting an unusually luxuriant moss mat with flowering Saxifragae, etc.

Phot. 2. Boulder-strewn slopes near the water in sheltered fjordhead region (p. 99). Even here the heathy vegetation is hardly noticeable from a distance, being rarely closed except in especially favourable depressions. Resting on a floating block of ice can be seen two ringed seals (*Phoca* sp.).
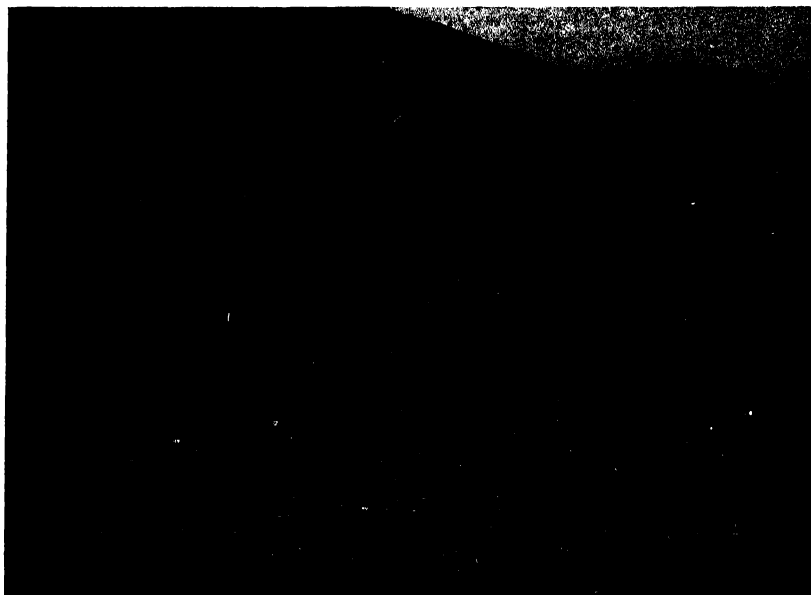
Phot. 3. Undulating *Dryas* 'barrens' chiefly of limestone, inland of Ny-London (pp. 86, 92). There is little stabilization of the surface by plants in exposed situations that are not manured; here in the sloping foreground the dynamic nature of the surface material is indicated by the tendency of the vegetation to form streaks (p. 92).
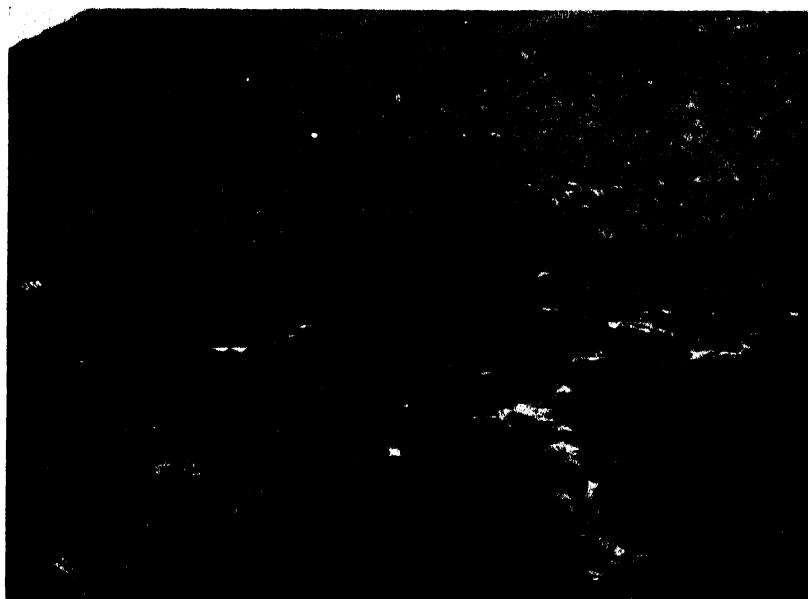
Phot. 4. Luxuriant herb-moss mat developed where water percolates in sheltered depression (pp. 86, 99). In the foreground, water coming from the slopes above has reached the surface and is seen running freely between some of the tussocks of vegetation, which by growth and the gathering of silt, etc., may become quite large and prominent; behind comes a tract of *Cassiope* heath, also snow-covered in winter, while in the background the slopes rise more steeply to the light-coloured 'barrens' of exposed situations.

of such high latitude (all less than 1000 miles from the Pole) the climate of Spitsbergen is relatively mild, being tempered by a branch of the Gulf Stream which approaches the south-west coast, with the result that along this coast the sea does not freeze over in an average winter except in the fjords. Nevertheless, during the winter the air temperature is rather low, and over a period of years no calendar month is entirely free from frost, although July and August may often be. During this brief summer—there is hardly any spring and autumn except in so far as these seasons are characterized by the rapid unfolding and inactivation, respectively, of life in the annual cycle—the temperature in the sun is often quite high on clear days, especially in the interior of the fjords, where 27 and 28° C. have been recorded (cf. Summerhayes & Elton (1923), who contribute some other interesting temperature data). It is well known that in Spitsbergen as in other arctic lands the fjord-head regions enjoy a much more continental, and to plant life more favourable, climate than does the coast (Pl. 6, Phot. 2).

So far as I have been able to determine no protracted meteorological observations have been made in Kongsfjord, but the following table shows the mean temperature for the different months over the period 1912–26 at Grönfjord (Green Harbour), situated in Isfjord a comparable distance from the coast but about 100 km. to the south-south-east and probably enjoying a slightly warmer but otherwise similar climate:

	Mean temp. in °C. 1912–26	Mean precipitation in mm. 1912–24
January	– 16·1	35
February	– 19·1	37
March	– 18·5	27
April	– 13·5	24
May	– 4·8	12
June	2·0	11
July	5·4	16
August	4·6	22
September	0·1	25
October	– 5·8	23
November	– 11·8	24
December	– 14·3	37
Yearly average – 7·6		Total for year 299

On most flat areas the snow lies generally from the middle of September until the middle of June, which leaves a growing season probably at the very most of only three months even for the plants on south-facing slopes where the snow melts first, and much less on most other areas, since frosts come regularly in early September. The fjord usually freezes up during the latter half of October, this 'sea' ice disappearing by the end of June.

The precipitation in Kongsfjord appears to be little known; but it is said, like that of other places in Spitsbergen, to be low and mostly in winter in the form of snow. (Some figures are given, in the table above, of the mean monthly and annual precipitation observed over a period of years at Grönfjord.)

The relative humidity tends to be very high owing to the lowness of the temperature, and foggy or cloudy days are all too frequent, especially near the coast. But once the temperature rises the actual small amount of water vapour present in the air can be easily absorbed and a very clear atmosphere result—a factor important in increasing the amount of direct insolation which the ground and vegetation can receive. Thus dark patches of vegetation in the sun can take on temperatures many degrees higher than the surrounding atmosphere; but this is only when the air is virtually still, which further emphasizes the importance of shelter and, through it, of local topography. These factors

and effects tend to be cumulative. On the other hand, in exposed places in the Arctic the air is rarely still and so high temperatures are rarely attained; such vegetation as can develop has, moreover, frequently to do without any protective blanket of snow in winter.

At Kongsfjord the 'midnight sun' lasts from 17 April to 27 August, the season of obscuration being from 23 October to 19 February.

(c) *Underlying rock, etc.*

The geology of the Kongsfjord region is rather complicated, the exposed rocks varying in type and chemical composition considerably from place to place. The mountains are composed for the most part of quartzite and mica schist (cf. Orvin, 1934), underlain by limestones. These last often appear at the surface near the coast, and in places on both sides of the fjord (e.g. at Ny-London and Ny-Aalesund) actually form small eroded cliffs by the sea. The lower slopes of the mountains are most frequently covered by long screes of talus blocks which have fallen from the crags above, but the coastal plains, at least where there are no small limestone cliffs by the sea, are generally covered by marine terraces of much-mixed material of varied composition, or, near the glaciers, by morainic deposits which are still more heterogeneous and variable. At Ny-London the hinterland and also the small cliffs by the sea are largely of limestone, although this is in places covered by gravelly marine deposits or moraines, while there is generally a greater or lesser number of large erratic boulders strewn about the smooth-worn, undulating surface (Pl. 7, phot. 3).

(d) *Water supply*

The available water not only varies from place to place with local changes in the topography, but it may also vary greatly at different periods in the summer, short as this is. The water supply is especially precarious on raised areas and porous rocks such as limestones. As the summer precipitation is with little doubt very small (see above) and most areas are almost constantly exposed to more or less drying winds, it follows that when once the water from snow melting *in situ* has disappeared, the plants on any area that does not lie in a marshy depression must depend for a continued supply mainly upon the results of melting of ground ice or larger patches of ice or snow situated elsewhere. Nevertheless, this slow melting serves to keep many areas abundantly supplied with water, so that in spite of the paucity of rain falling in summer the conditions are often very humid. Any gentle slopes below permanent snow patches or ice caps are generally plentifully supplied with water which, prevented from sinking far into the ground by bedrock or *tele* ('tjale', hard-frozen soil) or separated ground ice situated not far beneath the surface, percolates down near to or at the surface, over which it may spread so that the area comes to support a luxuriant moss or herb-moss mat in the form of a conical alluvial delta, from which deliciously cool water oozes in innumerable places (Pl. 7, phot. 4). On the other hand, raised hillocks or rocky outcrops of such porous material as limestone, or coarse morainic deposits, may have their surface almost bone dry from quite early in the summer. These when situated in exposed places near the sea have, as might be expected, generally the poorest vegetation of all.

(e) *Manuring by sea birds*

This factor cuts right across the others, promoting the development of quite luxuriant vegetation on almost any area that is not too dry (see foreground in Pl. 6, phot. 1).

The topography and degree of exposure matter little more than the nature of the sub-stratum, which matters hardly at all—cf. the situation on Akpatok Island and elsewhere in the Canadian Eastern Arctic (Polunin, 1935 and MS.). Even a shortage of water to any reasonable degree need not be damnatory, the effect being cumulative when once the vegetation has got a proper start, for the more moss or grassy vegetation that is produced the more will melting snow and other water be conserved. Even where there are no typical 'bird-cliffs' much of the plant food may be brought from the sea by birds. This was clearly the case at Kongsfjord, where many areas near the sea were obviously visited more or less regularly by flocks of feeding wildfowl. Here again the effect is cumulative, for the more luxuriant the vegetation is, the more the area will be visited and manured, and the more it is manured the more luxuriant will the vegetation become. Apart from such local manuring effects, which are rarely seen more than 2 or 3 km. from the sea, the biotic factor is probably less important in such high-arctic lands than almost anywhere else in the world, although in the sea itself life frequently abounds.

While the soil varies greatly in texture, mechanical components, and chemical con-stituents from place to place, it seems worth mentioning here one sample taken at random by Orvin (1934) from the uppermost layer of a seaside terrace in Kongsfjord. It was poor, brownish coloured and 'homogeneous', consisting of stone fragments and gravel with only very little earth. According to Orvin 'The earth does not contain humous substances worth mentioning with the exception of the uppermost stratum, which contained some thin root fibres':

From   0 to 25 cm. it contained 54% of gravel and stones.
  ,,   25 to 40 cm.   ,,   82%   ,,
  ,,   40 to 50 cm.   ,,   87%   ,,

Further investigation of the drier uppermost stratum (0–25 cm.) gave the following results as percentages, showing the material to be very poor in fertilizing agents:

N	0·09	Fe_2O_3	5·98
P_2O_5	0·04	Ignition loss	6·16
K_2O	0·05	Reaction pH	6·54
CaO	0·53		

The supply of 'available' nitrogen in the soil is in most areas very low or at least precarious in the Arctic. This may be due to the usual absence of Leguminosae and, it appears probable, to the relative inactivity, under the prevailingly low temperatures, of nitrifying and nitrogen fixing bacteria rather than to their actual absence (cf. Russell *et al.* 1940); on the other hand, denitrification may be quite rapid (Barthel, 1922), even at relatively low temperatures, and especially under excessively humid conditions (cf. Waksman, 1931). This scarcity of both inorganic and organic nitrogenous (and also probably to a lesser degree of phosphatic) food materials is abundantly illustrated by the much richer vegetation which appears wherever there is even the smallest tendency towards its being made good by manuring.

Although the soil in Spitsbergen is almost everywhere frozen to a great depth in winter, in summer the surface thaws out to a depth of 60 or 80 cm., and sometimes considerably more—especially on dark south-facing slopes catching the sun's rays at right angles, or where the ground is raised or consists of well-aerated, coarse dry sand.

(f) Snow and ice effects

Perhaps because factors belonging to this set are of little or no importance in temperate regions, unless it be on high mountains, they tend to be overlooked by workers not familiar with arctic conditions both in winter and summer. Nevertheless, the effects may be quite striking; they include the following around Kongsfjord as in most other high-arctic lands:

(1) In depressions where the snow drifts so deeply each winter that its disappearance only well on or even late in the summer drastically reduces the growing season, the plant populations are naturally of species able to exist and usually reproduce in the short time remaining before winter. This effect is additional both to the abundance of water produced on melting and to the good protection against cold and desiccation afforded by the snow, which is a remarkably effective insulator and, even where it lies relatively thinly and melts slowly, may profoundly modify the vegetation.

(2) Near existing glaciers whose recent recession has left bare areas, more or less marked zones of colonization are often visible, starting usually with a broad 'sterile' zone nearest the glacier. Such colonization appears, in some instances at least, to be sufficiently slow even on comminuted substrates to suggest that the time which has elapsed since any other area was left free from ice may be of significance in determining its present vegetation—a fact obviously true of many rock faces.

(3) The effects of repeated phasic changes, particularly of soil water to ice, attended as this is by a marked increase in volume, are many and various in the Arctic, and result in or are closely connected with such familiar surface phenomena as frost-shattering and comminution of rock, solifluction, frost-heaving, and 'polygon' formation of many kinds.

3. Notes on the vegetation around Ny-Aalesund on the south coast of Kongsfjord

The deserted coal-mining camp of Ny-Aalesund at the time of my visit sported a large wooden quay and was usually the point of landing of parties from pleasure cruises visiting the fjord. Unfortunately, I was only able to spend a few hours ashore at this place, during which the following few notes were taken.

Stretching behind the huts of the mining camp was a plain about 1½ km. wide, of flat areas and slightly rising slopes. The vegetation of this plain, although open and depauperate, was not as extremely scanty and reduced as on many areas in Spitsbergen. However, it was of high-arctic type in being dominated over considerable areas by *Saxifraga oppositifolia* and *Luzula confusa*, with *Dryas octopetala* or *Papaver radicatum* in some places and a little *Cassiope tetragona* in the most favoured habitats; thus it was rather reminiscent of Craig Harbour in Ellesmere Island (Polunin MS.), whereas farther north conditions tend to get markedly less favourable (Ostenfeld, 1923).

Avoiding areas which had evidently been disturbed by man, the following phanerogams were noted in a walk across this plain (27 July) to the scree slopes and glacier beyond; the frequency degrees given are rough and purely relative (authorities for plant names are given in the lists of 'Flora' at the end of the paper):

Saxifraga oppositifolia	v.a.–d.	Luzula nivalis	l.a.
Luzula confusa	f.–co-d.	Cerastium regelii	l.a.
Dryas octopetala	l.a.–l.d.	Cassiope tetragona	l.a.
Salix polaris	l.a.	Saxifraga caespitosa	f.–l.a.

Papaver radicatum*	l.	Pedicularis hirsuta	o.
Oxyria digyna	f.	Saxifraga cernua	o.
Gramineae as a whole	f.	Juncus biglumis	o.
Including Festuca rubra var. arenaria		Cerastium alpinum	o.
Deschampsia alpina		Sagina intermedia	o.
Puccinellia vahliana		Lycopodium selago	o.
Phippsia concinna		Carex rupestris	o.
P. algida × concinna?		Stellaria longipes	r.–o.
Poa, cf. arctica × pratensis	s.l.	Polygonum viviparum	r.
Drabae as a whole	f.	Silene acaulis var. exscapa	r.
Including Draba alpina		Cochlearia officinalis var. groenlandica	r.
D. oblongata		Saxifraga nivalis	r.
D. cinerea		S. hieracifolia	r.
D. fladnizensis s.l.		Lychnis apetala†	r.
Carex misandra	l.f.	Arenaria rubella	v.r.
Cardamine pratensis†	l.f.	Cardamine bellidifolia	v.r.

* Authorities for plant names are given in the lists on pp. 106 and 107.
† In depressions.

Of these *Lycopodium selago* and *Carex misandra* were associated with *Cassiope*; *Dryas* was on the tops of hillocks and *Papaver* on exposed ridges.

Cetraria delisei appeared to be by far the most abundant cryptogam on these plains, showing up more than any of the phanerogams present and making most areas look distinctly brown. This and other features indicate that the snow lies here, and melts relatively late.

The scree behind faced north-east. It was of jagged rock particles and in places almost entirely barren, hardly supporting even any mosses or crustaceous lichens. However, where it was more stable and some earth had collected near the surface, small plants of *Saxifraga oppositifolia* were fairly frequent and *Cerastium regelii* and Drabae occurred.

The flats and slightly rising slopes of the plains afforded three special habitat types:

(i) The works of man had caused the local and probably only temporary disappearance of the usual dominants and their replacement by a more luxuriant community usually consisting of tall grasses (including *Poa pratensis* up to 48·5 cm. high) with or without Drabae, large Cochleariae, *Saxifraga caespitosa* and other 'open soil' or nitrophilous plants, and sometimes carpets of *Tetraplodon wormskjoldii* or *Marchantia polymorpha*. *Ranunculus acris* L., *Stellaria media* (L.) Cyr. (flowering), *Rumex* spp. and several other interesting adventive plants have been noted here (see Høeg & Lid, 1929), probably brought in with fodder or litter for domestic animals when the mines were being worked.

(ii) There were low marshy areas near the settlement which were carpeted by a continuous investment of hygrophytic mosses in which grew much *Cardamine pratensis* (purely vegetative; leaves very variable in shape) and some *Saxifraga rivularis* and *Chrysosplenium alternifolium* var. *tetrandrum* as well as numerous Fungi. These appear to be the 'damp mossy flats' of Dobbs (1942), who in the second half of August 1936 noted among the 'larger fungi' occurring here *Tubaria furfuracea* (Pers.) W.G.Sm., *Omphalia umbellifera* (L.) Fr., *Dictyolus muscigenus* (Bull.) Quél., *Scleroderma aurantium* Pers., and *Russula* spp.

(iii) There were also hillocks or larger raised mounds, usually only about a metre high, but nevertheless showing definite horizons of vegetation presumably delimited in relation to the depth of the winter snow-covering and the time of its melting in summer. The flat tops of these mounds generally supported an open (one-quarter to one-half closed) fjellmark community of *Dryas octopetala* with large patches of light-coloured *Cetraria nivalis* indicating the poorness or absence of winter snow-covering just here. The sides of the mounds were generally dominated by *Cassiope tetragona*, with associated *Carex*

misandra, Lycopodium selago, Hylocomium alaskanum, and other plants not generally found in the surrounding areas. There were also to be seen on the sides of these mounds plentiful *Rhacomitrium lanuginosum* and dark brown *Cetraria* sp. or spp., but rarely more than a few scraps of *C. nivalis* just here. The indications were that a fair amount of snow collected around the sides of the mounds in winter and protected the plants from rapid changes in temperature and from desiccation, but that it melted relatively quickly in summer, allowing the water to drain away and the ground to dry and become warm. It is well known that such raised surfaces, when they catch the sun's rays more or less squarely, can take on surprisingly high temperatures even with the soil frozen only just below—especially when they are dark and the areas around are covered with snow. The observations of Wulff, reported by Ostenfeld (1923), make it clear that this important principle holds true on the northernmost known coasts as long as there is no wind.

As for the rest of the plain, it appears that it is generally well covered with snow in winter, and that because of its exposed nature and northerly slope, however slight the last may be, this snow melts relatively late in the summer. The ground is then left wet and cold for a long time, as, with the soil frozen not far beneath the surface, the drainage is extremely bad. Hence the vegetation is generally of high-arctic type, the chief plants being Saxifragae (chiefly *Saxifraga oppositifolia*), Luzulae (chiefly *Luzula confusa*) and *Dryas*, with *Oxyria, Salix polaris, Papaver* and Drabae as characteristic associates in some places. The plants are later in flowering than in many places even farther north: for instance, *Saxifraga oppositifolia*, which is always one of the very first flowers to appear in the Arctic a few days after the snow melts and then is soon over, was still flowering plentifully just here on 27 July in 1933. So were some of the Drabae, while *Cerastium regelii* and *Stellaria longipes* were still in bud. Among other indications that the place had a cool 'late' summer relatively unfavourable for plant growth was the fact that *Cardamine pratensis* did not appear to be flowering at all, as no buds were visible although numerous plants were examined. To be sure, this lack of 'cuckoo flowers' was also noticeable in some other parts of Spitsbergen, as it may be elsewhere (Polunin, 1940); but I have rarely if ever seen the species so plentiful, while apparently relying for propagation solely on vegetative means, as it was in 1933 at Ny-Aalesund.

On the other hand, the relatively exacting *Cassiope tetragona* occurred and even dominated favourable if very limited areas; and even the general vegetation seems to justify the placing by Summerhayes & Elton (1928) of this Ny-Aalesund area of Kongsfjord in their '*Cassiope* Zone' of medium vegetative luxuriance, for this vegetation was as a whole markedly less depauperate than that developed on many of the more exposed coastal regions of Spitsbergen.

4. The vegetation around Ny-London on the north coast of Kongsfjord

Just over the other side of the narrowest part of the fjord (see Fig. 1), where it is only about 4 km. wide, lies the deserted settlement of Ny-London, consisting of a few tumble-down (in 1933) huts and machine houses, the relics of yet another unsuccessful mining venture. Several days were spent here in early August, almost surrounded—as frequently in Spitsbergen, so it seems—by pointed, snow-capped mountains around whose sides run glaciers often right down to the sea (Pl. 6, phot. 1). From the ends of these fully

'active' glaciers huge chunks of ice would break with a loud rending crack and fall with a roar into the water, this 'calving' either producing an almost continuous stream of icebergs which floated down the fjord with the tide and finally out to sea, or, when the wind was onshore, filling the head of the bay with pieces of ice of all sizes. Seals of two kinds abounded here, and little puffing white whales (*Delphinapterus leucas* (Pallas)), but with sea birds generally less abundant than in many surrounding areas there was little save the inorganic forces of nature to disturb the vegetation; indeed, except on recently deposited moraines (see § 7 below), even proximity to a large glacier seemed usually to have little or no effect upon the nature of the plant communities developed.

As will be seen from the following account, the vegetation as a whole is considerably more luxuriant than at Ny-Aalesund, the seasons being apparently also earlier with the flowers mostly over by the end of July (in 1933). This is probably in the main due to the southerly aspect and frequently more sheltered situations provided by the rugged topography. The flora also seemed to be larger, due presumably to these same factors and to the chemical diversity of the geological substrate which included considerable areas of limestone. While some plants appeared to be restricted to soils of special mineral origin, or at any rate to grow better on them, the vegetation around Ny-London seemed to be fairly similar on the different rocks except for the case already mentioned, viz. the exposed limestone areas near the sea which supported extremely sparse *Saxifraga oppositifolia* or *Dryas* barrens (or, on the less exposed hinterland, somewhat richer fjellmark or polygon-inhabiting communities). Thus even if the flora tended to be enriched by an abundance of limestone, this was hardly true of the vegetation; indeed, in Kongsfjord it was the exposed limestone areas near the sea which supported by far the poorest vegetation encountered in the region. These exposed areas were not only remarkably reminiscent of the similarly exposed limestone plateau of Akpatok Island, Hudson Strait, in their general appearance of light-coloured plains spotted with dark-coloured tussocks of plants, but the phanerogam flora and general vegetation even after minute investigation of test areas was found to be almost identical, while the lichens appeared very similar. This is already suggested by a comparison of the lists given below from limestone areas at Ny-London with those given for Akpatok Island (Polunin, 1934, and cf. 1935); even where a species typical of one of these far-distant points is absent from the other, its place is generally taken by a nearly related or at least ecologically comparable species.

As is usual in arctic regions of locally varying topography, the vegetation varies drastically from place to place—often from one square decimetre to the next. We must confine ourselves to describing a few of the more outstanding communities.

(a) Saxifraga oppositifolia *barrens*

As on Akpatok Island and in other seaside situations this extremely reduced, high-arctic type of community is developed on small, wind-eroded hills by the side of the fjord. Most of those examined were of limestone. The surface varies in texture on different areas even when these are close together. It may consist of coarse, gravel-sized particles (from ½ to 3 cm. in diameter), or of sharp-cutting flakes of larger size but having a rough surface due to erosion by long exposure to rain, wind, and blizzards; or frost comminution may have gone much further and produced some soil at the surface, often showing stone circles or 'polygon' formations on flat areas (Pl. 8, phot. 6, in background),

or streaks due to solifluction on such slopes as are not too arid. Pl. 7, phot. 3 shows the sort of intermediate state (between polygons and streaks) to be seen on some rather slight slopes.

With the actual surface usually dry and probably unstable in the face of high winds the vegetation is extremely poor, generally consisting of occasional small scattered plants of *Saxifraga oppositifolia*—smaller and less frequent than those of *Dryas* in Pl. 7, phot. 3. The *Saxifraga* plants are rarely more than 10 cm. in diameter, although where *Dryas* occurs its tussocks may sometimes be much larger even on this type of terrain. As is indicated by the following list from one area, the associated vascular plants are few. Even cryptogams are little in evidence, although *Cetraria nivalis* may occur in any larger patches of higher vegetation and *Ochrolechia frigida* may sometimes be quite frequent; also, specks of crustaceous lichens are generally to be found on the larger stones:

Saxifraga oppositifolia	f.	Salix polaris	r.
Polygonum viviparum	r.–o.	Lychnis apetala	v.r. (1)
Dryas octopetala	r.	Draba alpina s.l.	v.r. (1)

In the less extremely exposed areas *Dryas* usually becomes more plentiful and a stony *Dryas* barren (Pl. 7, phot. 3) or fjellmark area (on comminution of more of the surface material) may be produced, with the entry of further herbs and of lichens including *Cetraria delisei*.

(b) Dryas *fjellmark*

This is again a typical arctic community. It is developed in most areas near the sea that, on the one hand, are not too exposed for the 'dominant' to grow relatively well or too dry to prevent frost comminution, and on the other hand are not suitable for the ecesis of the stronger-growing dominants of more favoured habitats. Needless to say the community, while always open, varies greatly with exposure and other conditions in different areas, not only in the degree of vegetative covering but also in floristic composition.

The examples listed were true fjellmark areas, consisting of rock particles of all sizes and including much fine grey mineral 'soil' from which the larger jagged pieces of rock stuck up conspicuously. The particles were chiefly of limestone origin, although there was considerable admixture of erratic material. The soil effervesced with acid except immediately beneath the larger patches of vegetation, where it was dark and humous but still neutral in reaction; elsewhere it was slightly basic (*p*H 7·5 as indicated by a B.D.H. pocket capillator) and without any evident horizons due to leaching or eluviation. There appeared to be some snow-covering in winter. Tussocks of *Dryas octopetala* up to 50 cm. in diameter and rising in the centre some 6 cm. above the surface of the ground formed the chief feature of the vegetation, except in some places where small Carices (*ca.* 20 cm. high) were so abundant as to make the whole area look straw-coloured from afar. These irregular patches of higher vegetation generally covered somewhere about half the surface, so that the general impression was of considerably greater luxuriance than in Pl. 7, phot. 3. The following is a composite list taken from two small areas:

Dryas octopetala	a.–d.	Arenaria uliginosa	r.
Saxifraga oppositifolia	f.–a.	A. ciliata subsp. pseudofrigida	r.
Carex misandra	o.–l.a.	Draba spp. (not flowering)	r.
C. rupestris	o.–l.a.	Cerastium alpinum	v.r.
C. nardina	r.–l.a.	Lychnis apetala	v.r. (1)
Polygonum viviparum	o.–f.	Draba subcapitata	v.r. (1)
Silene acaulis var. exscapa	o.	Braya purpurascens	v.r. (1)
Salix polaris	o.	Potentilla hyparctica	v.r. (1)
Saxifraga aizoides (flowering)	r.		

The smaller limestone fragments had their rough surfaces largely devoid even of crustaceous lichens, but on the larger pieces frequent black or yellow apothecia of

Lecidea spp. were visible, while the undersides of stones touching damp soil were colonized by an investment of Cyanophyceae. Any erratic piece of acidic rock tended to support far more lichens than the limestone. While they frequently formed a nidus for the roots of Carices, the *Dryas* tussocks were too closely compacted for mosses to flourish in them; consequently few were in evidence although those listed below were collected. Indeed, mosses occurred mostly as mere scraps that needed a lot of picking out, but nevertheless included an apparently undescribed species of *Campylopus*. Even lichens were of poor growth, and rather little in evidence although quite abundant (see list below). Thus where *Dryas* tussocks had died and left dark humous patches, these were in places grey or white with 'crumbling' lichens such as *Lecanora epibryon* and *Ochrolechia frigida*. Again, in the living tussocks *Cetraria nivalis* of fair growth occurred; and in their lee *Cetraria delisei* was often abundant and *C. islandica* (s.l.) frequent. Here the soil was often damp enough to support brown gelatinous colonies of *Nostoc commune*:

MUSCI:		LICHENES:	
Mnium orthorrhynchum		Ochrolechia frigida	a.
Bryum globosum var. ruberrimum		Cetraria delisei	a.
Trichodon oblongus		C. islandica s.l.	f.
Campylopus n.sp.		C. nivalis	f.
Hypnum bambergeri		Lecanora epibryon	f.
Pogonatum urnigerum		Stereocaulon rivulorum?	
Polytrichum sp.	o.	Caloplaca cinnamomea ('ex hab.')	
		Gyrophora sp.	v.r.

The above are 'early snow' areas with the flowers almost all quite over at the beginning of August in 1933. If succession can proceed further it may be expected to do so through increasing aggression and the local closure of some of the more favourable areas by *Dryas*, Carices, Luzulae and forbs, presumably to be dominated in the end by *Cassiope tetragona*, though it seems likely that on most of these areas, exposed and of limestone as they are, the vegetation has remained relatively stable for a long time.

In depressions having a good snow-covering in winter but which are stony and well drained, hence dry in summer, *Cetraria delisei* is often so abundant as to form a continuous dark-brown mat, while *Cassiope* of poor growth may frequently be seen 'entering' (see Pl. 8, phot. 5).* A deeper depression that was almost like a 'swallow hole' had its sides covered with an investment of *Salix polaris* and tangled, straggly *Saxifraga oppositifolia* with some associated *S. caespitosa*, *Polygonum viviparum*, *Cerastium alpinum*, *Luzula nivalis*, and *Oxyria*. The bottom, apparently of acidic material, supported a thin moss-mat including numerous dark tufts of *Grimmia doniana*, with some *Juncus biglumis* and *Equisetum variegatum* in a muddy corner.

The fjellmark developed on acidic rock in more or less exposed situations differs from that found on limestone chiefly in the greater abundance of lichens—especially of crustaceous types on the stones—and also of *Carex nardina* which may be very abundant and even co-dominant with the *Dryas*. From a distance these areas generally look straw-coloured, due to the abundance of dead and upstanding leaves of this and other Carices and often also of *Luzula confusa*, while raised areas where there is little or no snow-covering in winter are light yellow with *Cetraria nivalis*. Contrasted with this we have even the slightest depressions dark brown with a great abundance of *C. delisei*; and often associated with it there is some *Cassiope* (cf. above), so that the community forms a transition to the heathy areas to be described next.

* This photograph shows in the foreground some separate, upgrowing tufts of the *Cetraria*: such tufts may show almost perfectly regular radial growth and become detached and blown before the wind, so constituting a kind of arctic 'tumbleweed'.

(c) Cassiope *heath*

As on Akpatok Island and most of the less exposed regions of Spitsbergen, a dark heathy community dominated by *Cassiope tetragona*, consolidated by mosses and generally including some *Dryas*, is developed locally in the most favourable situations. But although the area is generally small the vegetation is rarely quite continuous all over it; the centre may be a closed mat, but towards the outside interruptions by stones and patches of uncolonized soil become more and more frequent. As in other high-arctic regions such *Cassiope* heath is developed best of all on sheltered non-limestone areas where the snow lies thickly in winter and 'spring', but where the southerly aspect allows of relatively rapid melting in summer and the slope ensures good drainage. Such was the example listed, not far above sea-level at Ny-London and occupying a pocket ending a ravine, sheltered on three sides and facing south. It was developed on a secondarily weathered morainic deposit such as is frequently found in Spitsbergen, the land of glaciers big and small; but although the soil in most places did not effervesce with acid it contained occasional limestone fragments and was exactly neutral as tested with my B.D.H. pocket capillator.

Above the surface of the soil, and generally about 3 cm. thick, lay a layer of litter and mosses which prevented rapid evaporation; below this the soil was damp, and for about 6 cm. dark-coloured and largely devoid of stones, although these were abundant below. *C. tetragona* of rather poor straggly growth was the dominant. It covered almost the whole area but never rose more than about 7 cm. above the surface of the cryptogam mat, and except where it was thickest was sufficiently open to allow a number of vascular plants to grow, the community giving the following considerable list from a 2 m. quadrat:

Cassiope tetragona	v.a.–d.	BRYOPHYTA:	
Salix polaris	a.	Dicranum groenlandicum	v.a.
Dryas octopetala	f.	Drepanocladus uncinatus	
Polygonum viviparum	f.	Brachythecium albicans	
Saxifraga oppositifolia	f.	Rhacomitrium lanuginosum	
Luzula nivalis	o.	Camptothecium nitens	f.
Carex misandra	o.	Hylocomium alaskanum	
Saxifraga cernua	o.	Polytrichum strictum	r.
Pedicularis hirsuta	o.	Ptilidium pulcherrimum	
Pedicularis lanata	o.	Odontoschisma macounii	
Cardamine bellidifolia	r.		
Oxyria digyna	r.	LICHENES:	
Draba alpina	r.	Cetraria delisei	v.a.
Silene acaulis var. exscapa	r.	C. islandica s.l.	a.
Saxifraga hieracifolia	r.	Ochrolechia frigida	a.
Equisetum scirpoides	r.	Cetraria nivalis	f.
Carex rupestris	r.	Cladonia elongata	f.
Cerastium alpinum	v.r. (1)	C. pyxidata	o.
Stellaria longipes	v.r. (1)		
Cochlearia officinalis var. groenlandica	v.r. (1)		

The cryptogams formed an almost continuous investment beneath the *Cassiope*, mosses being more abundant than lichens. Of them *Dicranum groenlandicum* was by far the most important species, covering almost half of the area and growing up to form luxuriant tussocks in places where the *Cassiope* was not too overwhelmingly dominant. Not far away lay a large patch of snow that was probably permanent from summer to summer, surrounded by a zoned series of 'late-snow' communities.

The *Cassiope* area itself seemed to be bared of snow relatively late in the summer, for its *Dryas* flowers were only just over on 5 August in 1933; moreover, much of the *Cassiope* does not flower at all but merely creeps along the surface of the cryptogam mat.

The community appears to represent the final stage of colonization on moraine areas, though under the present conditions succession to this stage can only proceed in especially sheltered situations. On the higher edges of the patch where the snow lies less deeply in winter and melts earlier each summer, lichens (including some *Cetraria nivalis*) were more abundant and the *Cassiope* was much more interrupted by *Dryas, Silene*, and other plants which can grow strongly only where the growing season is longer and competition from *Cassiope* less severe. Conditions here, and the attendant vegetation, are in many ways comparable with those occurring over considerable areas near the summits of the higher mountains of Norwegian Lapland (Polunin, 1936).

(d) Aquatic and lake-marginal communities

The aquatic and marginal communities of the numerous little tarns in exposed areas are extremely variable, exhibiting, as on Akpatok Island, drastic changes in the vegetation not only from tarn to tarn but frequently in closely contiguous areas in or around the self-same small body of water. To what extent the resulting populations may be due to the autogenic activity of early colonists, and thus be dependent upon the manifold hazards of effective dispersal, is open to conjecture as is the absorbing question of whether, with growth so very slow, the local communities will by convergence attain to a climatic climax (if such a thing is to be expected) before climatic change has rendered them obsolete. Here again I must confess myself sceptical, and inclined to look upon each different area as possessed of vegetationally different potentialities, so slow is vegetable turnover and so improbable any physiographic change sufficient to allow climatic and edaphic conformity over major areas.

Most frequently the water lay as little pools only a few decimetres deep even if they were many metres in diameter, in depressions in the rock surface scooped out by glaciers. The rock showed occasional cracks filled with frost-shattered particles, or depressions filled with damp soil supporting near the water various mosses (usually sterile), and such tiny vascular plants as:

Salix polaris	Polygonum viviparum
Saxifraga oppositifolia	Saxifraga aizoides (on limestone)
Equisetum variegatum?	Juncus biglumis

Around their margins these little tarns, which presumably persisted throughout the growing season, were being colonized by more or less pure beds of one or another of the following, the species often changing several times along a few metres of the same apparently uniform shore:

(i) *Alopecurus alpinus*, although this was not common.

(ii) *Eriophorum scheuchzeri* (most frequently).

(iii) *Eriophorum angustifolium* var. *triste* (less frequently) (Pl. 8, phot. 6, though this is of a peculiar case which will be described below).

(iv) *Colpodium fulvum* var. *effusum* f. *depauperatum*, chiefly in the more sheltered areas.

(v) *Carex saxatilis*, again only occasionally, forming a close sward but rarely flowering.

The grasses were able sometimes to colonize open water directly—where it was very shallow.

Other plants which may occur associated with the marginal beds, or on the almost bare stony or polygon areas that lay between them when they were discontinuous, as

was frequently the case, were as follows (the frequency degrees are purely relative as all the plants were local and merely casual):

Juncus biglumis	a.	Cochlearia (seedlings only)	r.
Cardamine pratensis (no flowers)	f.	Various grasses including *Deschampsia*	
Equisetum arvense	f.	*alpina* up to 35 cm. high (see tuft in	
E. variegatum	f.	foreground of Pl. 8, phot. 6)	
Ranunculus hyperboreus	o.		

Tall, coarse tussocks of the *Deschampsia* are especially characteristic of damp depressions in exposed situations as in Pl. 8, phot. 6. The *Ranunculus* grows especially well in the water, and with the leaves reaching up to and expanding on the surface constitutes the nearest approach to a 'floating leaf' type seen in Spitsbergen.

Small bodies of standing water were sometimes largely 'filled' with aquatic mosses such as *Calliergon giganteum* or marsh-puddle ones such as *Drepanocladus revolvens*, generally encrusted with diatoms and consequently dark brown except near the growing points. These mosses frequently formed a continuous investment at the bottom of shallow pools, aided by brown gelatinous Cyanophycean colonies and green or yellowish filamentous Algae—most often sterile *Zygnema* sp. or spp. On the beds of the deeper tarns in sheltered places there had frequently been formed a reddish brown, crusty deposit of dead and partially decomposed algal material bound by living aquatic mosses but including living *Nostoc* spp. and *Chroococcus turgidus*. In summer, gases are frequently liberated within or underneath such deposits as a result presumably of bacterial action, and, when the crust holds together sufficiently well, the whole may be buoyed up to or near the surface of the water—a most amusing phenomenon which I have noted also in other northern lands. The gases are easily liberated on puncturing the buoyed-up sheet of brown humous matter with a stick or stone, when great bubbles rise to the surface and the deposit sinks slowly to the bottom.

Pl. 8, phot. 6 illustrates another peculiar phenomenon, this time associated with freezing, that frequently occurs around small pools—a muddy rampart often raised 12 or 15 cm. and no wider than it is high. Most frequently—as in the example photographed—it was vegetated by pure *Eriophorum angustifolium* var. *triste*, while behind came barren polygons stretching to typical *Dryas* fjellmark on exposed limestone terrain. Very occasionally the relatively stable, raised muddy intervening tracts of large 'stone' polygons in damp situations may be vegetated by a 'line' (as in Pl. 9, phot. 7) of this same *Eriophorum*, whose fruiting axes are seen in addition to leaves of *Carex misandra* and axes of *Equisetum variegatum*, and where the foreground of the photograph is occupied by barren pieces of limestone covering the surface of the dynamic polygon area.

(e) Marshy areas

With the frequent drastic changes in topography and vegetation—and often in the latter without any apparent reason—marshy areas were of small extent and little importance around Ny-London. However, in one place in a depression by a stream not far behind the huts there was developed a luxuriant and wet, hummocky moss-tundra (as opposed to a flat 'mat') that seems worthy of note. The surface consisted of small low mossy tussocks up to 20 cm. high and 30 cm. wide, and coloured golden brown by the dominant moss (at this season). These tussocks were separated by marshy depressions of dark humus with frequent Cyanophycean colonies. The underlying soil was also dark and humous but effervesced with acid sufficiently to indicate a considerable admixture

Phot. 5. In foreground a sheltered depression in which snow collects and lies deeply in winter: it is clothed by *Salix polaris* and Carices, etc., with abundant *Cetraria delisei* (p. 93). In background is poorer vegetation with light-coloured lichens where there is little or no snow-covering in winter. The narrow ecotone between supports dark *Cassiope tetragona* which for good growth needs to be snow-covered in winter.
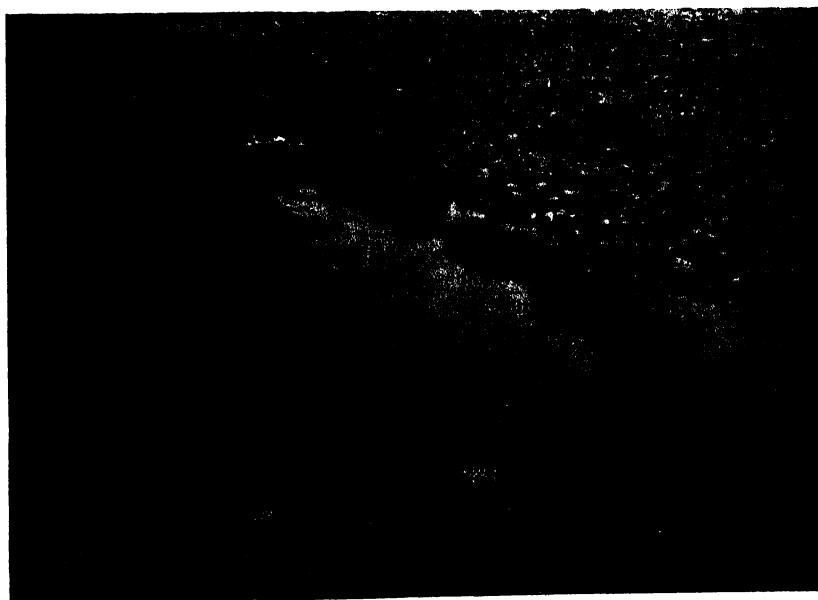
Phot. 6. Muddy rampart, associated with frost heaving, marked by dense belt of *Eriophorum angustifolium* var. *triste* (pp. 95, 96). The tall, light-coloured tussock in the water in foreground is of *Deschampsia alpina*. Around are barren 'stone' polygons (pp. 91, 96).

Phot. 7. Raised muddy intervening tract of polygon successfully colonized by band of *Eriophorum angustifolium* var. *triste* among whose axes can be seen some *Carex misandra* and much *Equisetum variegatum* (p. 96). Barren pieces of limestone occupy the surface of the polygonal area.

Phot. 8. *Saxifraga aizoides* tussock of remarkable solidity and dimensions— scale given by matchbox (p. 100). From this 'cushion' protrude leaves of *Polygonum viviparum*. To the right, above, can be seen a more normal, loose tussock of the *Saxifraga* flowering profusely.

of calcium carbonate; its pH was 7–7·5. This area, like several similar ones seen (sometimes even in exposed places) in different parts of Kongsfjord within easy reach of the sea, was frequently visited by northern eiders (*Somateria mollissima borealis*) and probably some geese. The introduction of nitrogenous and other food bodies by these wildfowl had had a considerable effect upon the vegetation. The luxuriant mossy tussocks supported the following vascular plants:

Poa arctica? (barren)	l.v.a.	Deschampsia alpina	o.
Polygonum viviparum	a.	Juncus biglumis	o.
Ranunculus hyperboreus	l.a.	Eriophorum scheuchzeri	o.
(in muddy depressions)		E. angustifolium var. triste	l.
Equisetum arvense	f.–l.a.	Cardamine pratensis (leaves only)	l.
Salix polaris	f.–l.a.	Saxifraga aizoides	r.
Equisetum scirpoides	f.	S. oppositifolia (1 seedling)	v.r.

Although a single species predominated, the mosses were many and considerably mixed, the most notable being the following:

Orthothecium chryseum	v.a.–d.	Drepanocladus intermedius
Campylium stellatum	a.	Tetraplodon wormskjoldii
Trichodon oblongus		Aulacomnium papillosum
Aulacomnium palustre		Drepanocladus revolvens
Camptothecium nitens		Calliergon giganteum var. cyclophyllotum

There was also another unnamed variety of *Calliergon giganteum* growing in or just above the water in the deepest depressions. Lichens were absent from the above luxuriant community, but a number of Fungi of various shapes and colours occurred, chiefly Agaricaceae. Their growth, like that of most other plants, was noticeably more luxuriant than at Ny-Aalesund, being in some instances almost comparable with that observed the same year at Longyear (cf. also Dobbs, 1942) and in other parts of Isfjord.

In some other examples of these nitrophilous mossy marshes there were tussocks growing up as much as 40 cm. above the general surface, often coalescing to produce raised areas several metres in diameter, having dry tops colonized by lichens where they were not too overwhelmingly dominated by *Salix polaris* or other phanerogams. The mosses themselves were most often 15–20 cm. thick above the squishy, brown humous core. This was frozen hard at a depth of about 45 cm. beneath the surface of the mosses, on whose dry tops occurred in one tract the following less hygrophytic vascular plants:

Salix polaris	l.v.a.	Equisetum scirpoides	r.
Saxifraga caespitosa	a.	Luzula nivalis	r.
S. oppositifolia	l.a.	Cerastium regelii	r.
Polygonum viviparum	f.	Cochlearia officinalis var. groenlandica	r.
Equisetum arvense	f.	(tiny)	
Puccinellia vahliana	o.	Saxifraga cernua	v.r. (1)
Draba alpina	r.	S. rivularis	v.r. (1)
Stellaria longipes	r.	Juncus biglumis	v.r. (1)

The majority of the above species were of poor growth, and it seemed that mosses could benefit more than higher plants from the slight increase in food substances, or perhaps compete better for them. *Aulacomnium palustre* was the chief species here, all the others being far less frequent:

Aulacomnium palustre	v.a.	Ceratodon purpureus var. brevifolius
A. papillosum		Timmia arctica
A. turgidum		Philonotis tomentella
Dicranum groenlandicum		Bryum sp. (barren)

The chief lichen was *Ochrolechia frigida*, while a few Fungi occurred. Like those from limestone areas, these lists show considerable conformity with those taken from similar habitats on Akpatok Island in spite of the great difference in geographical position.

5. VEGETATION OF A 'BIRD' ISLAND

No major 'bird-cliffs' inhabited by great numbers of guillemots or other sea birds were noted in the Kongsfjord region, but the largest of a group of islands (the Lovénöyane) near the head of the fjord was visited during seal hunting and found to be the nesting place of wildfowl, although largely deserted at that season (early August). These birds which nest on the ground prefer such small islands, for here they are safe from foxes. The nests in this instance were very numerous and placed close together, often within a metre or two of one another. The nitrogenous and other food materials deposited each year in the excreta, etc., of the birds had had a most profound effect upon the vegetation, whose luxuriance demonstrated abundantly the usual extreme poorness of the soil in this as in other arctic regions (see above, p. 87). Even the exposed rocks on the shore were largely covered with such lichens as *Physcia muscigena* (cf. Lynge, 1938), *Collema* sp. (sterile), and luxuriant *Caloplaca elegans* (cf. Akpatok Island), in which the orange colour of the *Caloplaca* predominated. Elsewhere the surface of the island was covered with a continuous thick moss mat (see Pl. 6, phot. 1, and cf. Akpatok) except on some raised areas where there were no nests. Even here the nutrient materials introduced by blown feathers and excreta, or left by scavengers, had frequently had some effect, for the *Dryas* community was often closed and included an abundance of *Carex rupestris* and other herbs not usually occurring in such areas. Indeed, there were to be found, as might be expected, all stages of gradation from the normal fjellmark and heath series to the extreme result of deflexion by manuring which yields a luxuriant moss-herb community (cf. Summerhayes & Elton, 1928).

The present moss mat was extremely thick and luxuriant, the feet in places sinking many centimetres into its gently undulating rich green or brown surface. It emitted a foul odour from the many undecomposed bird droppings that were still lying about. The mosses were intricately mixed but the chief species seemed to be as follows:

Camptothecium nitens	Paludella squarrosa
C. lutescens	Tetraplodon wormskjoldii
Hylocomium palustre var. julaceum	

They formed a sward too thick and luxuriant and probably too wet to allow many lichens to grow, but supported numerous fine clumps of the golden-flowered *Saxifraga hirculus* and white-flowered *S. caespitosa*, both in full bloom, and a number of other herbs including the following, of which only the *Arenaria* was flowering, actually very profusely:

Arenaria ciliata subsp. pseudofrigida	a.	Festuca rubra var. arenaria
Cardamine pratensis	a.	Poa arctica
Cochlearia (barren)	a.	P. abbreviata
Ranunculus pygmaeus	l.a.*	Cerastium spp.
Chrysosplenium alternifolium		Stellaria longipes
var. tetrandrum	l.	

In a region as remote and inhospitable as Spitsbergen the biotic factor is usually of little importance considering the area as a whole, especially as man, who has destroyed the natural vegetation almost everywhere else in the world, if he goes to Spitsbergen at all does so generally only temporarily to mine or to hunt. Thus all except a few very

* This occurrence of *Ranunculus pygmaeus* is in conformity with the habitat as described by Scholander (1934) for other parts of the Spitsbergen Archipelago but is very different from the usual one to which I have become accustomed in various other arctic and subarctic lands—see also *Bull. Torrey Bot. Club*, 71, p. 250, 1944.

small areas—usually to be measured quite comfortably in square decametres—remain to this day without showing the slightest sign of man's interference, although his advent may nevertheless have had a more considerable secondary effect upon the vegetation if we remember how greatly he has reduced the numbers of browsing animals (especially reindeer) and visiting wildfowl. However, the latter still abound and may have a very considerable ameliorating effect upon the vegetation of such areas as they visit at all regularly, as has been indicated above, while occasional smaller areas, where they go summer after summer to nest, generally come to have the most luxuriant, thick-matted vegetation of the whole region. I saw no reindeer in Kongsfjord in 1933, but plenty on and near the little-visited east coast when crossing the main island quietly alone.

6. THE VEGETATION OF A SHELTERED FJORDHEAD AREA

Towards the head of Kongsfjord, on the north shore between two 'live' glaciers which come down to the sea and discharge their material as icebergs breaking from precipitous cliff faces, is a stretch of land about $2\frac{1}{2}$ km. long which indicated by Summerhayes & Elton (1928) as supporting more advanced vegetation than the rest of the region, which except on the exposed ocean coast belonged to their 'Cassiope Zone'. This limited tract of 'Inner Fjord Zone' I indeed found to be both more luxuriantly vegetated than the environs of Ny-Aalesund and Ny-London, and inclusive within its flora of several relatively mesothermic plants that were not seen elsewhere in Kongsfjord. Thus, following Scholander (1934), has another 'old-time land-crab botanist' (as opposed to one who makes his observations from a seaplane!) been able to substantiate a further part of Summerhayes & Elton's tentative map 'showing the zones of climate and vegetation'.

This area lying in a side bay near the head of the fjord, with glaciers on either side and snow-capped mountains behind, is almost certainly the warmest and most sheltered part of Kongsfjord. Its south-facing slopes rise directly to the 1070 m. high Feiringfjell and there are other lofty peaks near by. Unlike most areas within the Cassiope zone, where this plant occurred merely in limited tracts in especially favourable localities, the gentle, boulder-strewn slopes nearest the sea (Pl. 6, phot. 2) were here largely covered with an irregular (but generally not quite closed, even between the boulders) heath of Cassiope with associated Dryas, Saxifraga oppositifolia, Salix polaris (with some S. reticulata) and many Carices. These last and the frequency of Sphagna (whose tussocks were sometimes quite large and aggressive) seemed to indicate the 'Inner Fjord Zone', although neither the heath nor the limited areas of Sphagna were quite as luxuriant as at Adventfjord in Isfjord about 100 km. to the south-east.

There also occurred, near the shore, areas of thick tussocky 'moss' studded with herbs, grasses, and variously coloured Fungi (and sometimes with Cladoniae and Cetrariae in the drier areas) like that described above from Ny-London but rather more luxuriant and extensive. These areas seemed again to depend upon the visits of wildfowl, for their grasses were often eaten down and the surface around trampled; but, with the area more sheltered and the substratum 'acidic', they differed from the Ny-London ones in supporting frequent luxuriant red or yellowish patches of Sphagna. These 'mosses' were generally characterized by an abundance of Salix polaris and were developed only on areas that had been kept well supplied with fresh percolating water by the melting of ground-ice or of snow on the mountains above. Frequently with such an area in the foreground

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there was a dark strip of *Cassiope* heath behind, and above this sheltered 'angle' an exposed ridge of *Dryas* fjellmark rendered light-coloured by *Cetraria nivalis*, etc. The upper part of the moss mat may also support *Salix polaris*, some grasses, Luzulae, *Pedicularis hirsuta* and a little *Cassiope tetragona*, with around a narrow strip of dark *Cassiope* heath, and above this the ecotone (of almost closed *Dryas* with *Salix polaris*, *Polygonum viviparum*, and Carices) to *Dryas* fjellmark as the steeper slope is ascended. In such manner are several of the main plant communities of the area frequently to be seen along a transect no more than 3 m. long!

The vegetation of this most favourable part need not be described at any length, as the communities were much like those of the parts of Kongsfjord already treated, except that they were almost always more luxuriant (but nevertheless only occasionally and very locally closed). However, a few notes may be offered on points of interest.

In the depressed centre of one area of *Cassiope tetragona* heath, whose light mineral soil, browned by humus, was slightly but distinctly on the acid side of neutrality (about pH 6·0), and whose 'late-snow' nature was further indicated by the abundance of *Cetraria delisei* and the total absence of *C. nivalis* as well as of *Dryas*, a good growth of *Cassiope hypnoides* was found. Later this charming micro-heath was seen actually dominating some small areas. It has only very occasionally been found in Spitsbergen before (although this may be partly due to its inconspicuous, moss-like habit), and is said to be confined to the west coast of the main island; indeed, this appears to be the northernmost 'find' in the world of this highly interesting and beautiful circumpolar species.

Again, the familiar *Tofieldia pusilla*, several tussocks of which were found the same day in the same most favourable part of Kongsfjord, had previously been recorded in Svalbard only from Isfjord, so this would appear to be a new 'farthest north' record for this very widespread species. The tussocks found in Kongsfjord were hard and compact and often 20 or 30 cm. across, consisting of a large number of the usual tiny rosettes pressed closely together—a habit also taken on by the related *T. coccinea* Richardson in its northernmost stations in Arctic America, viz. around lat. 77° 45′ N. in Greenland, and at lat. 74° 35′ N. on Devon Island.

A very similar habit was noted in some examples of *Saxifraga aizoides* growing in sheltered areas of damp fjellmark at Ny-London, where the tussocks sometimes approached 50 cm. in diameter and were close and hard and flowered but rarely (Pl. 9, phot. 8). When they did so it was almost equally all around—unlike the similar hard, domed tussocks of *Silene acaulis* var. *exscapa* which flowered chiefly (sometimes only) on the south-facing side, where the flowers so regularly came out first and most abundantly that the plant constituted an admirable compass (Polunin, 1939, see photograph).

Much of the *Salix* hereabouts has toothed leaves and, writes Mr Wilmott (*in lit.*), 'may be *S. herbacea × polaris*'. The toothing is generally most marked on luxuriantly growing, large-leaved examples in the most favourable habitats.

In this apparently most temperate as well as sheltered part of Kongsfjord, facing south and having the earliest seasons, the Salices already in the first week in August were taking on 'autumn tints' (at least in 1933). Except in areas which had only been left bare by the melting snow relatively late in the growing season, and whose plants had accordingly been checked in resuming full activity and were even in some instances still in flower, the leaves of *S. polaris* had their margins yellowing at this time while

those of *S. reticulata* were already a beautiful orange red and ready to drop off when jarred.

Some of the areas of unmelted snow or compacted névé still lying on the lower mountain slopes behind were distinctly reddish orange. The cause was not actually examined in this place, but instead of the usual 'red snow' Algae it may well have been the remains of marine Crustacea, etc., dropped by sea birds flying to and from their nests on the rocks above (cf. Summerhayes & Elton, 1923). No 'red snow' could be found far from these nesting sites, which occurred in many places although no typical 'bird-cliffs' were seen in Kongsfjord.

For rapid comparison with other regions a list was made of the plants seen during a walk of about ½ km. straight up from the shore to the foot of the mountain behind. This rough belt transect, listed in 'bird's-eye' fashion, included again the majority of the outstanding habitats of the area, and was as follows; it contrasts significantly with the shorter list (in spite of the transect being there about three times as long) made at Ny-Aalesund, where conditions are less favourable and the flora and vegetation correspondingly more reduced. The frequency degrees are again purely relative; they indicate the general 'show' or impression of abundance or importance made by each species in the area transected:

Cassiope tetragona	v.a.	Draba (other spp.)	o.
Dryas octopetala	v.a.	Including Draba alpina s.l.	
Salix polaris	l.v.a.	D. subcapitata	
Saxifraga oppositifolia	a.	D. nivalis	
Carex rupestris	a.	Luzula nivalis	r.
C. misandra	a.	Cochlearia sp.	r.
Polygonum viviparum	f.	Puccinellia vahliana	r.
Luzula confusa (calcifuge)	f.	Arenaria rossii	r.
Silene acaulis var. exscapa	f.	Stellaria humifusa	r.
Salix herbacea × polaris? (see text, p. 100)	f.	Equisetum variegatum	r.
S. reticulata	l.f.	Cassiope hypnoides	r.
Poa arctica (and apparent hybrids)	l.f.	Saxifraga nivalis var. tenuis	r.
Equisetum scirpoides	o.–f.	S. stellaris var. comosa	r.
E. arvense	o.	Cardamine bellidifolia	r.
Pedicularis hirsuta	o.	Eriophorum angustifolium var. triste	r.
Stellaria longipes	o.	E. scheuchzeri	r.
Juncus biglumis	o.	Cerastium alpinum	r.
Deschampsia alpina	o.	Lycopodium selago	r.
Draba fladnizensis s.l.	o.	Oxyria digyna	r.
Carex nardina	o.	Phippsia algida (very small)	r.
Saxifraga cernua	o.	P. concinna	v.r.
Arenaria uliginosa	o.	Cardamine pratensis (leaves only)	v.r.
Saxifraga caespitosa	o.	Sagina intermedia	v.r. (1)
Pedicularis lanata	o.	Saxifraga rivularis	v.r. (1)
		Arenaria sajanensis	v.r. (1)
		Lychnis apetala	v.r. (1)

This list, in spite of the small area covered—which itself was but incompletely searched—includes about one-third of the c. 135 species of vascular plants (c. 129 phanerogams) known to occur in Spitsbergen. Lichens and mosses were everywhere much in evidence, including *Cetraria delisei* which was perhaps the most abundant plant in the whole area and made the vegetation look brown in many places, and *C. nivalis* which was very plentiful on raised prominences. It seems probable that if this area had been predominantly of calcareous rock its vegetation would have been markedly less luxuriant (cf. Acock, 1940).

It may have been noted that in the transect listed above, which was stated to include the majority of the chief habitats of the area, there was neither mention of salt marshes nor inclusion of salt-marsh species. With the small tide range and sheltered situation,

and the usual absence of a suitable shore and of waves and spray, little or no shore marginal zonation of vegetation was to be seen, and few exclusively maritime vascular plants were observed, except for small reddish beds of *Puccinellia phryganodes* where the shore was muddy enough. Nor was any significant difference noted between the vegetation or amount of humus deposited on the lowest slopes near the sea and on those occurring farther back, whatever may have been the local oscillations in level in recent times (see Walton, 1922; Summerhayes & Elton, 1923; Vogt, 1933). Where local topography allowed, and the shore was not too shingly and dynamic, there was generally a line of mossy tussocks supporting phanerogams to mark the limit of the ordinary neep tides, so that the highest spring tides dumped the remains of marine Algae among the *Dryas* and Saxifragae growing there—especially *Saxifraga caespitosa*, and *Phippsia algida* where the situation was lastingly damp enough. The *Cassiope* generally started about two feet above this highest 'drift line'. The shore was in most places shingly and barren, and even where there were rocks the fucoids that grew on them were all small and usually confined to sheltered crevices—probably due to grinding by ice. It seems likely that, where suitable conditions occur, there will be found salt-marsh vegetation of the type described by Walton (1922) and Dobbs (1939), though I would expect to find associated plentiful *Stellaria humifusa* and *Carex ursina*, which are two of the most characteristic and important plants of such habitats in many other parts of Spitsbergen as well as in Greenland (Gelting, 1934; Seidenfaden & Sørensen, 1937) and the Canadian Eastern Arctic (Polunin, 1940 and MS.), but which appear to have been very little (in the case of the *Stellaria*) and not at all (the *Carex*) in evidence in the vicinity of Cape Napier (Walton, 1922; Dobbs, 1939; Acock, 1940). The probable explanation why Michelmore (1934) found *Carex ursina* only once in eastern Svalbard, remarking that 'it is not possible to say why [it was]...so local', is that this species is practically confined to markedly saline habitats, whose communities Michelmore lumped with so many others under his heading 'Ordinary Fjaeldmark' (*sic*).

7. SUCCESSION ON SOME RECENTLY BARED AREAS

Two examples will now be given of the recolonization of bared areas in the Kongsfjord region, since the phenomenon is important for the light it may throw upon the problems of succession. The first example had a natural agent of nudation, namely, a receding glacier which left morainic deposits in its wake. A belt transect outwards from the glacier gave the following results:

(i) Near its edge the glacier bore frequent conical 'drumlins' of dark gravelly material. These rose generally only a few feet above the surrounding glacier and had ice not many centimetres beneath their surface, which included much finer soil but was wet and cold, and, in all of the places examined, as completely devoid of any recognizable macroscopic form of plant life as the surface of the glacier itself.

(ii) A stream of cold water, joined by frequent tributaries coming from crevasses in the ice, ran along the side of the glacier. It, too, appeared to be absolutely barren, although streams in other less unfavourable situations generally supported a considerable abundance of filamentous green Algae attached to the stones forming their beds.

(iii) Then came a stretch of unevenly deposited and ill-assorted morainic sand, gravel, and boulder material which was also devoid of any macroscopic plants. In spite of the

situation near the relatively warm head of the fjord its surface was cold and wet, with ice not far below; nor was there any evident stabilization of the surface by diatoms or other Algae. Its barrenness in spite of its considerable breadth (at least 100 m.) illustrated drastically the extremely inhospitable nature of the 'habitat' for colonization by plants; for on the one hand the glacier must presumably have taken at least several summers to recede so far, and on the other hand there were plenty of well-vegetated areas not far away from which migration could have taken place even if birds are rarely seen in such situations and wind is the only agent of transportation normally operative. Hence the suggestion is that cold and lack of stability of the surface (cf. Summerhayes & Elton, 1923) are the chief factors preventing ecesis just here, although in other places many vascular plants (including trees in Alaska) grow near to or actually upon glaciers— in the latter case of course on the overlying soil. The margins of the glaciers of Spitsbergen may recede and advance almost from year to year, but on the whole they seem to be receding (according to Dr Hermann Ritter—voce).

(iv) Next came another and larger stream, and afterwards another stretch of unevenly deposited morainic material, having ditches and ridges running in almost all directions but mainly down towards the sea. On this area, about 50 m. from the last stream, the first plants were found on patches of earth between boulders. They were mosses and consisted of very occasional small tufts of Bryum nitidulum (which was fruiting in some instances) and other Bryum sp. or spp. which were barren. That these most easily dispersed plants should be the first colonists suggests that dispersal may possibly be the master factor inhibiting recolonization, in contradiction to what has been suggested above. Certainly the problem is far from settled. As for soil or substrate composition, it is thought unlikely that this can be a limiting factor in the recolonization of these recent moraines, for the material comes from almost all kinds of rock (though the samples tested in this case contained little $CaCO_3$), and much of it is finely pulverized, while in winter sufficient vegetable matter such as dead leaves probably gets blown over the snow and on to the surface of the glacier for its deposits to contain an appreciable amount of humus. Near these first mosses were some pieces of Cetraria nivalis which had presumably been blown from neighbouring vegetated areas but had now taken 'root' and appeared to be flourishing, having squamules up to 6 cm. long that must have been at least several years old.

(v) Just behind these earliest of evident cryptogam colonists (microscopic examination would probably have revealed quite numerous unicellular Algae in some places even quite near to the glacier) the first angiosperms were met with: these were quite frequent seedlings of Saxifraga oppositifolia and one or two of Draba sp. A few metres farther on was a tuft of Saxifraga oppositifolia some 10 cm. in diameter that had flowered earlier in the summer. Here the fine-textured, clayey earth in sheltered places behind boulders was quite efficiently bound by mosses (chiefly barren Bryum sp. or spp.) with some grey lichens and brown 'jelly' colonies of Cyanophyceae, although it was so wet as to allow the feet to sink several centimetres into it.

(vi) Behind this there were signs of visitation by small birds, and angiosperms rapidly became more frequent, with Saxifraga oppositifolia (f.) by far the most important. Indeed, except for S. caespitosa (r.), which was noted several times (generally as seedlings but once or twice in flower), the following associates were found only once each in an area of many square metres, although all were of good healthy growth and either in

flower or fruit: *Lychnis apetala, Poa* cf. *arctica* × *pratensis* (s.l.), *Saxifraga cernua*; and *Cochlearia officinalis* var. *groenlandica*.

(vii) The first area in which vegetation became really noticeable was situated about 200 m. from the edge of the glacier. A square on about 10 m. was listed as follows:

Saxifraga oppositifolia	f.	Arenaria rubella	(1)
S. caespitosa	o.	Carex nardina	(1)
Cerastium alpinum	o.	Cochlearia officinalis var. groenlandica	(1)
Drabae	o.	Salix polaris	(1)
Including Draba alpina s.l.		Deschampsia alpina	(1)
D. subcapitata		Poa, cf. arctica × pratensis s.l.	(1)
D. cinerea and ?hybrids		Saxifraga cernua	(1)
Sagina intermedia	o.	Papaver radicatum	(1)
Braya purpurascens	r.	Stellaria longipes	(1)
Oxyria digyna	r.		

Although cryptogams were abundant their growth was so poor that the ground between the higher plants looked almost devoid of them.

This sparse open community passed, with the ever-increasing abundance of *Saxifraga oppositifolia*, to a 'barrens' type of area ('dominated' by this same *Saxifraga* mixed with *Luzula confusa*, *Silene acaulis* var. *exscapa*, *Salix polaris*, and many cryptogams) and finally through a fjellmark area (dominated by *Cassiope* and *Dryas*, which appeared to enter simultaneously just here, with abundant *Carex rupestris*) to the scrappy heath (dominated chiefly by *Cassiope*, *Dryas*, *Salix* and *Carex* species—see above) that covered so much of the most favoured part of Kongsfjord.

Thus, following glacial retreat, plant establishment appears to have been difficult and colonization slow in this instance—even in comparison with others that I have observed for example in Wijdefjord (northern Spitsbergen) and at Dundas Harbour on Devon Island in the Canadian Arctic Archipelago. Such activities, and the ensuing succession, depend for their speed (and, I believe, also their course) on a great multiplicity of factors both known and unrecognized.

The second example of a recently bared area had a very different agent of nudation: just around the huts of Ny-London man has created new habitats. Perhaps the most interesting of these—again because of its bearing on the problems of succession—was a long heap of gravelly soil, including many larger stones and some limestone material, on which was to have been constructed a miniature railway leading down to the sea from a mine. It was said to have been made 18 years previously and was now colonized by the following 'open soil' and other plants, among which *Saxifraga oppositifolia* was again by far the most important, forming, in the absence of competition, luxuriant patches which in some instances attained a diameter of ½ m. and which in places half covered the area:

Saxifraga oppositifolia	a.–v.a.d.	Papaver radicatum	o.
Braya purpurascens	f.	Dryas octopetala (small tussocks only)	r.
Cerastium alpinum	f.	Arenaria rubella	r.
Drabae	f.	Silene acaulis var. exscapa	r.
Including Draba alpina		Puccinellia vahliana	r.
D. fladnizensis s.l.		Carex nardina	v.r. (1)
Lychnis apetala	o.	Saxifraga aizoides	v.r. (1)
Polygonum viviparum	o.	Oxyria digyna	v.r. (1)
Salix polaris	o.		

The flowers of almost all the plants were over by the first days of August in 1933, the area being raised and hence freed from snow early in the summer—if indeed it ever had a proper covering even in winter. The small size of the tussocks of *Dryas*, even relatively

to those in more exposed situations, suggested that the growth of this important colonist was rather slow. The ground between the higher plant colonists was almost bare of cryptogams, few mosses and practically no lichens being evident.

The sides of the bank, themselves evidently snow-covered in winter and well drained in summer, had already a few scraps of *Cassiope tetragona*, and much more *Carex nardina* as well as some *C. misandra*.

There can be little doubt that, although in some 18 (at most 20) years the plants had been able to make little more 'show' than they would in temperate regions have made before the end of the second summer, colonization in this case had been much quicker—probably very much quicker—than on the moraines described above. On the other hand, if we allow for the presence of limestone favouring the somewhat calcicole *Dryas* and especially *Saxifraga aizoides* at Ny-London and its absence allowing the calcifuge *Luzula confusa* to enter the moraine, the angiosperm colonists in the two cases compare very closely, in spite of the difference in soil texture and temperature and in water conditions. These colonists are for the most part typical 'open soil' plants that flourish only in the absence of competition (cf. Polunin, 1939, 1943); they do not appear to be types that are especially easily dispersed, unless it be by small birds transporting the seeds—a phenomenon concerning whose importance in the Arctic we have, unfortunately, very little knowledge.

8. THE FLORA

Below is given a list of all the land plants that have been identified from the material which I collected (or in a very few instances only saw) in Kongsfjord in 1933; as has already been said this list is probably far from a complete 'flora' even as regards the phanerogams, while the cryptogam lists are merely fragmentary.

The vascular plants are named and arranged according to my 'Botany of the Canadian Eastern Arctic, Part I: Pteridophyta and Spermatophyta' (1940), with such occasional modifications as are necessary to cover additions and recent nomenclatural changes (cf. Polunin, 1943), in which latter instances sufficient of the synonymy is given to guide the reader in Arctic botanical literature. For help with their identification I am much indebted to Mr A. J. Wilmott of the British Museum (Nat. Hist.). The mosses and few liverworts were kindly identified by Mr W. R. Sherrin of the British Museum, the Bryales being named and arranged, as far as was found possible, according to the appropriate parts of *Die natürlichen Pflanzenfamilien* (2nd ed., vols. 10 and 11, 1924–5), and the Sphagnales and Hepaticae being very few indeed. The lichens were identified by the late Prof. Bernt Lynge of Oslo; Macrolichens are arranged according to his paper of 1938 in which he already published many but not all of my records, and the Microlichens are added as far as they were named by Prof. Lynge, whose intended and eagerly awaited paper on them appears never to have been completed. The few fresh-water Algae mentioned were identified by Mr G. Tandy of the British Museum. To each one of these gentlemen, as well as to Dr J. Ramsbottom, the Keeper of Botany, for the facilities of his Department, and to the Christopher Welch Trustees for a grant towards the expenses of my expedition, and to the Faculties of Oxford and Yale Universities for leave of absence, my sincere thanks are due and warmly offered. The specimens are mostly in the possession of the British Museum, though many remain in my own working herbarium and 'a good set of duplicates' of the lichens is in the Botanical Museum of Oslo (cf. Lynge, 1938).

PTERIDOPHYTA
Equisetum arvense L.
E. variegatum Schleich.
E. scirpoides Michx.
Lycopodium selago L.
SPERMATOPHYTA
Alopecurus alpinus Sm.
Deschampsia alpina (L.) Roem. & Schult.
Phippsia algida (Soland.) R.Br.
P. algida × concinna
P. concinna (Fries) Lindeb.
Poa abbreviata R.Br.
P. arctica R.Br. and var. vivipara Hook.
? P. arctica × pratensis s.l.
P. pratensis L., s.l.
P. alpina L. vivipara
Colpodium fulvum (Trin.) Griseb. var. effusum (Lange) Polunin f. depauperatum (Nathorst) Polunin (Colpodium malmgreni Anders.)
Puccinellia phryganodes (Trin.) Scribn. & Mer.
P. vahliana (Liebm.) Scribn. & Mer.
Festuca rubra L. var. arenaria (Osbeck) E. Fries
Eriophorum scheuchzeri Hoppe
E. angustifolium Honck. var. triste Th. Fr.
Carex nardina E. Fries
C. maritima Gunn., s.l.
C. parallela (Laest.) Sommerf.
C. ursina Dewey
C. rupestris All.
C. misandra R.Br.
C. bigelowii Torrey ex Schwein.
C. saxatilis L.
Luzula nivalis (Laest.) Beurl.
L. confusa Lindeb.
Juncus biglumis L.
Tofieldia pusilla (Michx.) Persoon (T. palustris of authors, T. borealis (Wahlenb.) Wahlenb.)

Salix reticulata L.
S. polaris Wahlenb.
? S. polaris × herbacea L.
Oxyria digyna (L.) Hill
Polygonum viviparum L.
Silene acaulis (L.) Jacq.
var. exscapa (All.) DC.
Lychnis apetala L.

Cerastium alpinum L., s.l. and incl. s.str.
C. regelii Ostenfeld
Stellaria longipes Goldie
S. humifusa Rottb.
Arenaria ciliata L.
subsp. pseudofrigida Ostenf. & Dahl
A. humifusa Wahlenb.*
A. rubella (Wahlenb.) Sm.
A. rossii R.Br. apud Richardson
A. uliginosa Schleich. apud Lam.†
A. sajanensis Willd. apud Schlecht.
Sagina intermedia Fenzl
Ranunculus hyperboreus Rottb.
Ranunculus sp.
R. pygmaeus Wahlenb.
Papaver radicatum Rottb.
Cochlearia officinalis L. var. groenlandica (L.) Gel. and var. arctica (Schlecht.) Gel.
Cardamine bellidifolia L.
C. pratensis L.
Draba alpina L., s.l. and incl. s.str.
D. oblongata R.Br.
D. subcapitata Simmons
D. fladnizensis Wulfen, s.l.
D. nivalis Liljebl.
D. cinerea Adams
Braya purpurascens (R.Br.) Bunge apud Ledeb.
Saxifraga rivularis L.
S. cernua L.
S. caespitosa L. and f. uniflora (R.Br.) Engler & Irmsch.
S. stellaris L. var. comosa Retz.
S. hieracifolia Waldst. & Kit.
S. nivalis L. and var. tenuis Wahlenb.
S. aizoides L.
S. hirculus L.
S. oppositifolia L.
Chrysosplenium alternifolium L. var. tetrandrum Lund
Potentilla hyparctica Malte (P. emarginata Pursh 1814, not Desf. 1804)
Dryas octopetala L.
Cassiope tetragona (L.) D. Don
C. hypnoides (L.) D. Don
Pedicularis lanata Cham. & Schlecht.
P. hirsuta L.

The above list has some glaring gaps which it seems probable could be filled during any future summer visit to Kongsfjord. Already, in addition, Resvoll-Holmsen (1927) reports *Petasites frigidus* Fr. ‡ and *Taraxacum brachyceras* Dahlst. from Kongsfjord, while Eilif Dahl of Oslo once told me that *Dupontia fisheri* R.Br. has been observed growing in the vicinity of Ny-Aalesund; I seem to have missed *Dupontia* there, though I have made no less than thirty-seven collections of it in other parts of Spitsbergen. *Arenaria humifusa* Wahlenb. is a new find of outstanding interest*.

BRYOPHYTA: see also Lindberg (1867) and Berggren (1875); cf. Arnell (1900) and H. N. Dixon (various papers especially in *Bryologist*) for more recent accounts of the mosses of other parts of the main island of Spitsbergen, and W. Watson (*J. Bot., Lond.*, **60**, pp. 327–30, 1922) concerning liverworts.
Sphagnum fuscum (Schimp.) Klinggr.
S. rubellum Wils.
Trichodon oblongus Lindb. (Ditrichum tenuifolium var. oblongum (Lindb.) Hagen)

Ceratodon purpureus Brid. var. brevifolius Milde
Campylopus sp.
Dicranum groenlandicum Brid.
D. schisti Lindb. (D. Blyttii of authors)
Grimmia doniana Sm.
Rhacomitrium lanuginosum (Hedw.) Brid.
Tetraplodon wormskjoldii (Hornem.) Brid.
Bryum globosum Lindb. var. ruberrimum Dixon
B. nitidulum Lindb.
Bryum sp., another (barren)

* *Fide* A. J. Wilmott, 1943. New to the flora of Spitsbergen—see *Nature, Lond.*, **152**, p. 451, 1943, and cf. *Proc. Linn. Soc. Lond.*, Session 154, Pt. 2, p. 118, 1943.

† Only once before confirmed from any part of the Spitsbergen Archipelago (Scholander, 1934).

‡ Confirmed by a specimen in the British Museum labelled 'Island at the fundus of King's Bay...coll. M. A. Fenton, 1911.'

Mnium orthorrhynchum (Brid.) Br. & Schimp.
Aulacomnium palustre (Hedw.) Schwaegr.
A. papillosum (C. Müll.) Lesq. & James
A. turgidum (Wahlenb.) Schwaegr.
Paludella squarrosa (Hedw.) Brid.
Philonotis tomentella Mol.
Timmia arctica Kindb. (T. austriaca of authors)
Campylium stellatum (Hedw.) Lange & C. Jens.
Drepanocladus uncinatus (Hedw.) Warnst.
D. revolvens (Sw.) Warnst.
D. intermedius (Lindb.) Warnst.
Hygrohypnum palustre (Hedw.) Loeske
    var. julaceum (Br. & Schimp.) Loeske
Calliergon giganteum (Schimp.) Kindb.
    and var. cyclophyllotum (Holz.) Grout
?Scorpidium scorpioides (Hedw.) Limpr.
Camptothecium lutescens (Hedw.) Br. & Schimp.
Tomenthypnum nitens (Hedw.) Loeske
    (Camptothecium nitens (Hedw.) Schimp.)
Brachythecium albicans Br. & Schimp.
Orthothecium chryseum (Schwaegr.) Br. & Schimp.
Hypnum bambergeri Schimp.
Hylocomium alaskanum (Lesq. & James) Kindb.
Pogonatum urnigerum (Hedw.) Beauv.
Polytrichum alpinum Hedw.
P. hyperboreum R.Br.
P. strictum Banks

Odontoschisma macounii (Aust.) Underw.
Ptilidium ciliare Hampe
P. pulcherrimum (Web.) Hampe
Marchantia polymorpha L.

LICHENES: see also Lynge (1938, and earlier papers
    therein cited)
Collema sp. (sterile)
Solorina bispora Nyl.
Cladonia rangiferina (L.) Web.
C. mitis Sandst.
C. elongata (Jacq.) Hoffm.
C. pyxidata (L.) Fr.
Stereocaulon sp. (probably rivulorum Magnusson)
Gyrophora sp.
Cetraria islandica (L.) Ach., s.l., or C. crispa (Ach.)
    Nyl.
C. delisei (Bory) Th.Fr.
C. nivalis (L.) Ach.
C. cucullata (Bell.) Ach.
Dactylina ramulosa (Hook.) Tuck.
Alectoria nigricans (Ach.) Nyl.
Physcia muscigena (Ach.) Nyl.
Lecidea spp.
Lecanora epibryon Ach.
Ochrolechia frigida (Sw.) Lynge
Caloplaca cinnamomea (Th.Fr.) Oliv.
C. elegans (Link) Th.Fr.

ALGAE. An accident befell all the marine and most of the fresh-water Algae which I gathered in Kongsfjord; only the following can be recorded:

Chroococcus turgidus (Kütz.) Naeg.
Nostoc commune Born. & Flah.

Nostoc (another sp., sterile)
Zygnema sp. (sterile)

FUNGI. Among the larger and more conspicuous agarics and parasitic forms a fair number were collected but, like most of the Algae, they appear to have been lost. Quite numerous species occurred; a few of the larger ones, found growing 'on the damp mossy flats at Ny-Aalesund' a few years later and identified in the British Museum, are reported by Dobbs (1942). The Micromycetes, on the other hand, are relatively well known from the careful examination of herbarium specimens of vascular plants by the seemingly indefatigable Lind (1928), who mentions 8 among the less well represented species as having been collected at Kongsfjord, and lists a further 43 as widespread and common in West Spitsbergen: these would seem likely to occur in Kongsfjord, whence indeed not a few are represented in my own collections of vascular plants.

REFERENCES

Acock, A. M. (1940). Vegetation of a calcareous inner fjord region in Spitsbergen. *J. Ecol.* **28**, 81–106.

Arnell, H. W. (1900). Beiträge zur Moosflora der Spitzbergischen Inselgruppe. *Öfv. K. (Sv.) Vet.-Akad. Förh.* **57**, 99–130.

Barthel, C. (1922). Recherches bactériologiques sur le sol et sur les matières fécales des animaux polaires du Groënland septentrional. *Medd. Grønland,* **64**, i, 1–75.

Berggren, S. (1875). Musci et Hepaticae Spetsbergenses. *K. Sv. Vet.-Akad. Handl.* N.S. **13**, no. 7, pp. 1–103.

Dobbs, C. G. (1939). The vegetation of Cape Napier, Spitsbergen. *J. Ecol.* **27**, 126–48.

Dobbs, C. G. (1942). Note on the larger Fungi of Spitsbergen. *J. Bot., Lond.,* **80**, 94–102.

Gelting, Paul (1934). Studies on the vascular plants of East Greenland between Franz Joseph Fjord and Dove Bay (lat. 73° 15′–76° 20′ N.). *Medd. Grønland,* **101**, no. 2, pp. 1–340.

Høeg, O. A. & Lid, J. (1929). Adventive plants in Spitsbergen. *K. Norske Vidensk. Selsk. Forh.* **59**, 176–8.

Lind, J. (1928). The Micromycetes of Svalbard. *Skr. Svalb. og Ishavet,* no. 13, pp. 1–61.

Lindberg, S. O. (1867). Förteckning öfver mossor, insamlade under de svenska expeditionerna till Spetsbergen 1858 och 1861. *Öfv. K. (Sv.) Vet.-Akad. Förh.* **23**, 535–61.

Lynge, Bernt (1938). Lichens from the West and North Coasts of Spitsbergen and North-East Land collected by numerous expeditions. I. The Macrolichens. *Skr. Norske Vidensk.-Akad.* .I. Mat.-Naturv. Kl. 1938, no. 6, pp. 1–136.

Michelmore, A. P. G. (1934). Botany of the Cambridge Expedition to Edge Island, S.E. Spitsbergen, in 1927. Part II. The vegetation. *J. Ecol.* **22,** 156–76.

Orvin, Anders K. (1934). Geology of the King's Bay Region, Spitsbergen. *Skr. Svalb. og Ishavet,* no. 57, pp. 1–195.

Ostenfeld, C. H. (1923). The vegetation of the north coast of Greenland based upon the late Dr. Th. Wulff's collections and observations. *Medd. Grønland,* **64,** 9, 221–68.

Polunin, Nicholas (1934). The vegetation of Akpatok Island. Part I. *J. Ecol.* **22,** 337–95.

Polunin, Nicholas (1935). The vegetation of Akpatok Island. Part II. *J. Ecol.* **23,** 161–209.

Polunin, Nicholas (1936). Plant succession in Norwegian Lapland. *J. Ecol.* **24,** 372–91.

Polunin, Nicholas (1939). Arctic plants in the British Isles. *Nature, Lond.,* **144,** 352–4; see also *J. Bot., Lond.,* **77,** 270–4, 1939, for 'Enumeration of the species and varieties'.

Polunin, Nicholas (1940). Botany of the Canadian Eastern Arctic. Part I, Pteridophyta and Spermatophyta. *Canada: Department of Mines and Resources, Nat. Mus. Bull.* no. 92, pp. vi + 408.

Polunin, Nicholas (1943). Contributions to the Flora and Phytogeography of south-western Greenland: an enumeration of the vascular plants, with critical notes. *J. Linn. Soc. (Bot.),* **52,** 349–406; see also *Proc. Linn. Soc. Lond.,* 154th session, pt. 2, pp. 117–18, 1943, for 'Some phytogeographical problems concerning the area'.

Polunin, Nicholas (MS.). Botany of the Canadian Eastern Arctic. Part III, Vegetation and ecology. *Canada: Department of Mines and Resources, Nat. Mus. Bull.* (publication to proceed after the war).

Resvoll-Holmsen, H. (1927). *Svalbards Flora.* Pp. 1–56. Oslo.

Russell, R. Scott (1940). Physiological and ecological studies on an arctic vegetation. III. Observations on carbon assimilation...on Jan Mayen Island. *J. Ecol.* **28,** 289–309.

Russell, R. Scott *et al.* **(1940).** Physiological and ecological studies on an arctic vegetation. II. The development of vegetation in relation to nitrogen supply and soil micro-organisms on Jan Mayen Island. *J. Ecol.* **28,** 269–88.

Scholander, P. F. (1934). Vascular plants from Northern Svalbard with remarks on the vegetation in North-East Land. *Skr. Svalb. og Ishavet,* no. 62, pp. 1–153.

Seidenfaden, Gunnar & Sørensen, Thorv. (1937). The vascular plants of Northeast Greenland from 74° 30′ to 79° 00′ N. lat. and a summary of all species found in East Greenland. *Medd. Grønland,* **101,** no. 4, pp. 1–215.

Summerhayes, V. S. & Elton, C. S. (1923). Contributions to the ecology of Spitsbergen and Bear Island. *J. Ecol.* **11,** 214–86.

Summerhayes, V. S. & Elton, C. S. (1928). Further contributions to the ecology of Spitsbergen. *J. Ecol.* **16,** 193–268.

Vogt, T. (1933). Late-Quaternary oscillations of level in Southwest-Greenland. *Skr. Svalb. og Ishavet,* no. 60, pp. 1–44.

Wager, H. G. (1938). Growth and survival of plants in the Arctic. *J. Ecol.* **26,** 390–410.

Waksman, S. A. (1931). *Principles of Soil Microbiology.* Second Edition. Pp. xxviii + 894. London.

Walton, J. (1922). A Spitsbergen salt marsh: with observations on the ecological phenomena attendant on the emergence of land from the sea. *J. Ecol.* **10,** 109–21.

R E V I E W S

RECENT PAPERS ON SOILS AND VEGETATION IN CEYLON

(1) **de Rosayro, R. A. (1943).** The soils and ecology of the wet evergreen forests of Ceylon. I, II. *The Tropical Agriculturist (Ceylon)*, **98**, pt. 2, pp. 4–14; pt. 3, pp. 13–35, with plates 1–13.

(2) **Joachim, A. W. R. and S. Kandiah (1943).** Studies on Ceylon Soils. XVI. The chemical and physical characteristics of the soils of adjacent contrasting vegetation formations. *The Tropical Agriculturist (Ceylon)*, **98**, pt. 2, pp. 15–30, with plates 1–6.

(3) **Senaratna, J. E. (1943).** Patana burning with particular reference to pasturage and wet patanas. A preliminary note. *The Tropical Agriculturist (Ceylon)*, **98**, pt. 4, pp. 3–16, with plates 1–4.

The general features of Ceylon vegetation as influenced by the diversity of climate and elevation for which the Island is conspicuous are well known yet, despite the opportunities offered, very few detailed studies of the different plant communities have been undertaken. The papers under review, by members of the Ceylon Forestry and Agricultural Departments, are a welcome addition to the literature available.

(1) In the first part of this paper a general account of the topography and climate of the wet evergreen forests is given, followed by a classification of the soil types. This is largely based on the author's earlier paper—'Soils of the wet zone forests of the Matara, Galle and Kalutara districts'—in *The Tropical Agriculturist*, vol. **92** (1939). Seven soil series are recognized, principally according to the distribution, size, and frequency of the gravel and stone constituents of the B and C horizons. They are distinguished as: I, Alluvial soils; II, Residual non-gravelly loams; III, Residual (Chomogenous) gravelly loams, with three subseries; IV, Soils with a zonal gravel layer; V, Swamp (clayey) soils; VI, Shallow, truncated and bouldery soils; and VII, Fernland (*kekilla*) soils, characterized by a well-defined raw or acid humus layer and associated specifically with the consociation of the fern, *Gleichenia linearis*, sometimes with *Imperata arundinacea*. But in the true forest soils also the conclusion is reached (p. 11) that 'the relationship between these Soil Series, forest communities and the dominant height growth of the tree layer is clearly demonstrated. The degree and rate of growth are conditioned more by the physical properties of the soil...than by the actual analytical composition of the soils, which does not vary appreciably'. This can be illustrated by a review of the different vegetation types, which are described in detail in the second half of the paper.

The description of plant communities follows the headings (briefly defined) of 'high forest', 'low jungle', 'scrub jungle' and 'fernland and grassland'. In each case, the ecological status is indicated according to Clements' (*J. Ecol.* 1936) terminology.

HIGH FOREST COMMUNITIES. 1. Dipterocarpus *Community*. This is the most striking forest type, in which the single species, *hora* (*Dipterocarpus zeylanicus**), may form as much as one-half of the entire tree layer. More rarely, *bu-hora* (*D. hispidus**) may also occur but this species is less gregarious in habit. Near rivers and streams, *diya-na* (*Mesua thwaitesii**) becomes prominent and in steeper sites, *kataboda* (*Durio zeylanicus*). The community is a well-stocked one with a good height growth for the dominant of up to 150 ft. Regeneration of *hora* is good in the seedling stage, but the author notes that advance growth and pole stages are usually lacking, probably on account of the closeness of the canopy leading to insufficient illumination. The most typical development of this community occurs on the moist, well-drained riverain alluvia of series I; it is found also on soils of series II and the better drained subseries (i) of series III. However, there is abundant evidence that in the past the *hora* community was much more extensive and that it was, in fact, the true climax for the Wet Evergreen Forest tract as a whole. Its subsequent restriction to the moister, more favoured situations is traced to the gradual deterioration

* Indicates Ceylon endemic species.

of soil conditions resulting from shifting (*chena*) cultivation and over-exploitation; in its present ecological status it is therefore to be regarded as a *post-climax*.

II. Mesua-Doona *Community*. A second well-defined community is predominantly composed of *na* (*Mesua ferrea*), *diya-na* (*M. thwaitesii**), *dun* (*Doona zeylanica**), and *yakahalu-dun* (*D. trapezifolia**), in various combinations. It occurs typically at the higher altitudes between 1500 and 3000 ft., on steep, bouldery slopes with soils of series II or series III, *i*. Under these conditions it is probably a true *climax*; in the vicinity of water courses a *post-climax* stage can be recognized in the association between *diya-na* and *hora*. In the community as a whole, regeneration of the principal species is abundant, especially of the *Doona* spp. The dominant height growth is usually more than 100 ft.

II (*a*). The Durio *and soft-wooded species faciation*. A local faciation within the former, practically confined to the higher forests of the Adam's Peak Range and with *kataboda* (*Durio zeylanicus*) as the predominant species, also *Doona congestiflora**, *Myristica dactyloides*, and *Palaquium petiolare**.

III. Campnosperma *and other species Community*. Another community of the Adam's Peak Range, with *aridda* (*Campnosperma zeylanicum**) representing a little over a half of the total stock. The stocking is dense and pole stages are abundant. The soil belongs to sub-series *ii* of series III and is commonly rather shallow with frequent exposures of slab rock. In view of these conditions, the community is to be regarded in part as a *sub-climax* dependent on the restricted development of the soil profile. An active agency in its maintenance at this stage is believed to be a dieback associated with an unidentified fungus attack at the base of the trees, for which the soil condition is a pre-disposing factor. The dominant height growth is restricted to 80–100 ft.

IV. *The* Vitex-Wormia-Chaetocarpus-Anisophylla-(Dillenia) *Community*. A mixed community occurring throughout the lower altitudes, or below about 750 ft. The principal species are *milla* (*Vitex pinnata*), *diya para* (*Wormia triquetra**), *hedawaka* (*Chaetocarpus castanocarpus*), *welipenna* (*Anisophyllea cinnamomoides**), and, except in one district, *godapara* (*Dillenia retusa**). The dominant height growth is poor, usually 75–100 ft. only, and the stocking and general appearance is also inferior to the communities previously listed. The usual occurrence is on soils of Series III, *ii* and *iii*, and Series IV. On account of the general accessibility of these forests, and evidence of past interference, they are to be regarded either as a biotically controlled *sub-climax*, or as a *sub-sere* successional to the climax *Dipterocarpus* and *Mesua-Doona* communities. As with the latter a soft-wooded faciation is also recognized at the higher altitudes. This is predominantly characterized by *Myristica dactyloides*, *badulla* (*Semecarpus gardneri**), and *atamba* (*Mangifera zeylanica**).

Low Jungle Communities. The most important of these is the *Aporosa-Chaetocarpus-Vitex-Anisophyllea* community which occurs on bouldery or exposed sites showing the shallow truncated soils of series VI. The height growth usually does not exceed 60 ft. In addition to biotic (human) interference, the local condition of severe exposure to monsoonal winds is recognized as a contributory factor in the maintenance of this community as a *disclimax* or *faciation* of the preceding. Other communities of minor status are dominated by the palm, *katu-kitul* (*Oncosperma fasciculatum**) and the overgrown shrub, *galkaranda* (*Humboldtia laurifolia*), respectively.

Scrub Jungle Communities. These are regarded as the earliest successional stages in the re-colonization of abandoned *chena* clearings. Initially, the shrubby *associes* of *Hedyotis fruticosa*, *Melastoma malabathricum*, and *Osbeckia aspera* is found; later, such tree species as *Wenlandia notoniana*, *Macaranga peltata* and *Trema orientalis* make their appearance and a gradual transition is effected to low jungle.

Fernland and Grassland Communities. Specifically associated with soils of series VII, characterized by a surface layer of raw humus and often,·as a result of desiccation, by a hard layer of ferruginous gravel immediately beneath, serving as an effective barrier to the establishment of seedlings. These communities are described and illustrated in more detail by Joachim and Kandiah (see below). They are regarded as *disclimaxes*, maintained by periodical firing.

De Rosayro's paper ends with a useful Tabular Summary showing the several communities, their soils, chief undergrowth species, regeneration, and ecological status, and is illustrated by two maps, graphs of rainfall data, twenty-three diagrams of soil profiles and ten photographs.

* Indicates Ceylon endemic species.

(2) The 'Studies on Ceylon Soils' by A. W. R. Joachim and his collaborators have been appearing in *The Tropical Agriculturist* since 1935. In this instalment, the problem of the transition, often very abrupt, from jungle to the various grassland (or fernland) communities adjacent, is considered in relation to differences in the soil type. Three such communities are dealt with, namely the wet and dry *patanas* at high elevations, the *kekillas* of the wet low-country, and the *damanas* (*talawas*) or parklands of the semi-dry low-country. As far as the first two of these are concerned, de Rosayro's conclusions are upheld, namely that they represent biotic climaxes maintained by firing. Such is also the opinion of the majority of workers concerning similar communities in other tropical countries. The *patana* soils are chiefly differentiated by their much lower replaceable base content, greater acidity, and higher water-holding capacity, moisture equivalent, etc.; these differences are not appreciable in the *kekilla* soils. Both groups, as would be expected, show well-marked surface humus layers, with relatively high carbon/nitrogen ratio. These soil characters are regarded as largely derived from the difference in vegetation, in the maintenance of which they are of secondary importance only. In the case of the *damana* vegetation, however, the effect of soil differences may be of more primary significance, the *damana* soils being shallower and bearing every evidence of impeded drainage, associated with considerably higher content of exchangeable magnesium, as compared with adjacent forest soils. Thus, despite the prolonged dry season, the effect of fire in preventing the succession to jungle may be much less pronounced than in the other two communities considered.

The paper is illustrated by six plates which give a good idea of the contrasting vegetation types in the different climatic regions.

(3) In J. E. Senaratna's paper, the practice of *patana* burning is considered from the point of view of soil erosion and of the effect on the quality of the grazing as determined by the stage in the succession. Limited experimental observations on the Bopatalawa *patanas* at 5000 ft. elevation (rainfall 104 in.) indicate that burning well in advance of the heavy rains has no deleterious effect on soil erosion. The chief value of the paper lies in its full discussion of the principles underlying the practice of veld burning in S. Africa and in its tentative recognition of stages in grassland succession in Ceylon analogous with those of the former country. These are as follows, viz.: (*a*) *Aristida* spp. dominant (confined to the dry zone and not represented on the *patanas*), (*b*) *Themeda tremula*, *Chrysopogon zeylanicus*, *Arundinella* spp., *Ischaemum* spp., etc. dominant; (*c*) the *mana*-grass stage, dominated by *Cymbopogon confertiflorus*. It is stage (*b*) that provides palatable grazing, whereas the later stage (*c*) is of very little value. The beneficial effect of firing is to arrest the succession in the earlier, useful stage.

In the past much theorizing has been indulged in to account for the origin of the Ceylon *patanas* (see Pearson, in *J. Linn. Soc.* **34**, 1899), and it is to be hoped that this short paper will be the forerunner of detailed ecological investigations whereby the successional development of this fascinating and extensive vegetation type may be fully worked out.

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Fritsch, F. E. *The Structure and Reproduction of the Algae.* Vol. II. 939 pp., Frontispiece, 336 figs. and 2 maps. Cambridge University Press.

This second volume marks the completion of Prof. Fritsch's work on the algae. It deals with the Phaeophyceae, Rhodophyceae and Myxophyceae, and is therefore to a much larger extent concerned with marine forms and also with forms of more specialized types somewhat more remote from the main, channels of plant development. Nevertheless, Prof. Fritsch is able to demonstrate a general tendency in these groups also to show possible serial relationships with heterotrichous origins as is markedly the case in green and yellow-green algae. As the book deals primarily with structural and reproductive peculiarities of the algae, a review of the contents might be regarded as somewhat out of place in this *Journal*. The complete work is, however, of such botanical importance that it ought certainly to be noticed in these pages. Its completeness of reference is such that it must long remain the necessary work of reference on the subject, and the integration achieved by the author among the multitudinous details of algal life history is alone sufficient to make it a noteworthy scientific performance.

In both plants and animals there is constantly evident a tendency for the simpler forms to show a much closer relationship between their life cycles and the habitat conditions than is evident among more advanced organisms. The algae are particularly of interest from this point of view, as there is clear evidence that their reproductive cycles are often determined wholly or in part by varying habitat conditions, as, for example, in the simpler Phaeophyceae. Thus the study of their reproduction can hardly be adequate unless it also includes detailed reference to the habitat conditions. Not the least of the services rendered by this book is the collection of references to the ecology of algae, particularly of the marine forms. Indeed, in order to avoid repetition, a preliminary chapter is devoted to such features as seasonal occurrence, geographical distribution and the distinctions between the subaqueous habitats in fresh-water and marine conditions. Considerable emphasis is placed on the exposure characteristic of marine types of littoral zonation, a feature lacking on fresh-water shores. The effects of light and its absorption, chromatic adaptation and sun and shade forms are all dealt with separately under the groups. It is probably correct to emphasize this distinction on British coasts with a large tidal range. We might anticipate that the effects of water movement and of exposure will predominate as ecological factors, whereas in subtropical and enclosed seas the light conditions are doubtless of prime importance. Enough has been said, perhaps, of the contents to indicate that this volume is not without ecological interest. Certainly, it is a valuable summary of much of the available information.   W. H. P.

Rayner, M. C. and Neilson-Jones, W. *Problems in tree nutrition.* Pp. 184, 27 Plates, 11 figs. London: Faber and Faber, Ltd.

This book consists of the series of papers on the mycorrhizal relations of trees (particularly of *Pinus*) that originally appeared in *Forestry* and the *Journal of Agricultural Science* between 1936 and 1942. The original papers are given without material alteration. Three things may, therefore, be said about it.

First, as these papers have already been reviewed at some length in this *Journal* (**31**, 41, 1943), no further reference to their subject-matter is necessary. In the second place, it will undoubtedly be a very great convenience for ecologists, for foresters and for botanists in general to have the papers in this compact form without the need to search for them in the separate volumes of the original journal. Lastly, however, one must doubt whether the form most suitable for original publication is equally acceptable when the papers are grouped in book form. It is inevitable that they appear to lack integration, and the original form is rarely that which will have its appeal to the widest class of reader. Nevertheless, ecologists, in particular, will find this volume to be of great convenience, and from this point of view the enterprise of the publishers is to be commended.   W. H. P.

The supply of paper and increased cost of printing, rather than any shortage of original contributions continue to limit the size of the *Journal*. Indeed, the steady flow of research work on animal ecology during the war has been a surprise to the editors. It suggests that there will be a notable expansion of activity when normal conditions are established; and that a considerable increase in circulation of the *Journal* will be needed to meet the cost of publishing even the pick of this work.

The present number contains the Society's important report (prepared by a Committee under the chairmanship of Prof. A. G. Tansley) on 'Nature conservation and nature reserves', which has already been printed in the *Journal of Ecology*; four original papers; two book reviews; 107 'Notices of Publications on the animal ecology of the British Isles', prepared as usual by a voluntary group, at present of eight people; and the Society's accounts for 1943.

J. Davidson, of the Waite Agricultural Institute in South Australia, analyses the growth rates at different temperatures of various life stages of flies and a moth (from the published experiments of other workers) and shows that they are adequately fitted by a special form of Pearl and Reed's logistic curve. He also discusses the formulae that had been previously proposed for the same purpose. F. L. Vanderplank described experiments in the bush in Tanganyika, to find out the preferences of the tsetse-fly *Glossina palpalis* for different mammalian hosts, such as domestic animals, lions, baboons, porcupines, etc. The order of preference empirically determined bore, on the whole, little relation to the taxonomic position of the animals: man came low on the list (though not quite at the bottom), so that the presence of alternative 'baits' may be important in assisting his partial immunity.

James Fisher and H. G. Vevers present the second and concluding part of their monograph on populations of the North Atlantic gannet (*Sula bassana*), with a summary of regional and total trends in numbers, showing decrease from 1834 to 1894, and subsequent increase and spread up to the present figure, estimated at $165,600 \pm 9500$ in 1939. Most of this cycle can be explained by changes in the intensity of human exploitation. The authors suggest that numbers will go on increasing with the protection that is now given to most of the breeding colonies. They give evidence that small colonies have low breeding rates.

K. Radway Allen gives the fourth section of his very thorough study of the early stages of the salmon (*Salmo salar*), with a detailed description of smolt migration in a river in Caithness. Although waves of movement occurred in the population, there was much individual variability in activity. Migration depends on age and growth (mostly at two years old), and such factors as water rising and temperature.

There are reviews of Lack's population study of the British robin; and of Soper and Wilson's monographic account of the introduction of the African malaria-carrier *Anopheles gambiae* into Brazil and its subsequent elimination by control measures.

CHARLES ELTON

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PAPERS OF ECOLOGICAL INTEREST RECEIVED

Beard, J. S. The natural vegetation of the Island of Tobago, B.W.I. *Ecol. Monogr.* **14**, 135, 1944.

Beard, J. S. Climax vegetation in Tropical America. *Ecology,* **25**, 127, 1944.

Chapman, V. J. A study of the botanical processes concerned in the development of the Jamaican shore-line. *J. Linn. Soc. (Bot.),* **52**, 407, 1944.

Chapman, V. J. A study of the environment of *Avicennia nitida* Jacq. in Jamaica. *J. Linn. Soc. (Bot.),* **52**, 448, 1944.

Chapman, V. J. The morphology of *Avicennia nitida* Jacq. and the function of its pneumatophores. *J. Linn. Soc. (Bot.),* **52**, 487, 1944.

Chapman, V. J. Methods of surveying *Laminaria* beds. *J. Mar. Biol. Ass. U.K.* **26**, 37, 1944.

Chapman, V. J. Regional plant ecology in the United States. *Nature, Lond.,* **154**, 42, 1944.

Cooper, Wm. S. Contributions of botanical science to the knowledge of postglacial climates. *J. Geol.* **50**, 8, 1942.

Cooper, Wm. S. An isolated colony of plants on a glacier-clad mountain. *Bull. Torrey Bot. Cl.* **69** (6), 429, 1942.

Deevey, Ed. S. Additional pollen analyses from southern New England. *Amer. J. Sci.* **241**, 717, 1943.

Deevey, Ed. S. Pollen analysis and history. *Amer. Sci.* **32**, 1, 1944.

Fenton, E. Wyllie. Some observations on heart rot in conifers from an ecological point of view. *Forestry,* **17**, 49, 1943.

Fenton, E. Wyllie. The algal vegetation of certain Bog Hall Farm soils. *Proc. Bot. Soc. Edinb.* **33**, 67, 1943.

Fina, A. L. de & Sordelli, A. Un Ano (1937) de Determinaciones Semanales, etc. *Agronomia,* **31**, 127, 1942.

Gardiner, A. C. Measurement of phytoplankton population by the pigment extraction method. *J. Mar. Biol. Ass. U.K.* **25**, 739, 1943.

Godwin, H. Neolithic forest clearance. *Nature, Lond.,* **153**, 511, 1944.

Godwin, H. Age and origin of the 'Breckland' heaths of East Anglia. *Nature, Lond.,* **154**, 6, 1944.

Good, R. D. On the distribution of the primrose in a county. *Naturalist,* 1944.

Hart, T. John. Phytoplankton periodicity in Antarctic surface waters. *Discovery Reports,* **21**, 261, 1943.

Hoffman-Grobety, A. Étude d'une tourbière de la terrasse de Riedmatt dans le massif du Karpf. Für das Jahr 1942. *Veröff. Geobot. Inst. Rübel,* **19**, 1942.

Juday, Chancey. The summer standing crop of plants and animals in four Wisconsin lakes. *Trans. Wisc. Acad. Sci.* **34**, 103, 1942.

Kalela, A. Die Ostgrenze Fennoskandiens in pflanzengeographischer beziehung. *Veröff. Geobot. Inst. Rübel,* **20**, 1943.

Knoche, W. Ideas sobre los Fundamentos Bioclimaticos. *An. Soc. Argentina Est. Geog.* **7**, 99, 1943.

Knoche, W. Clima de las Metropolis y de interiores. *Rev. Meteorol.* **2**, 46, 1943.

Knoche, W. La Influencia Humana sobre el Clima (La Formacion del Desierto). *Soc. Argentina Est. Geog.* **6**, 1943.

Laessle, A. M. The plant communities of the Welaka area. *Univ. Florida Publ. (Biol. Sci.),* **4**, 1, 1942.

Ludi, Werner. Über rasengesellschaften und alpine zwergstrauchheide in den Gebirgen des Apennin. *Veröff. Geobot. Inst. Rübel,* **19**, 1942.

Newton, Lily. Pollution of the rivers of west Wales by lead and zinc mine effluent. *Ann. Appl. Biol.* **31**, 1, 1944.

Oliver, F. W. Some remarks on desert dust storms. Printed for the Desert Committee, Ministry of Agriculture, Cairo.

Polunin, N. Some proposals for the wartime use of plankton. *Chronica Bot.* **7**, 3, 1943.

Potzer, J. E. & Van Engel, W. A. Study of the rooted aquatic vegetation of Weber Lake, Vilas County, Wisconsin. *Trans. Wisc. Acad. Sci.* **34**, 149, 1943.

Rübel, Eduard. Begriffe und systeme. *Veröff. Geobot. Inst. Rübel,* **19**, 1942.

BRITISH ECOLOGICAL SOCIETY

SYMPOSIUM ON 'THE ECOLOGY OF CLOSELY ALLIED SPECIES'

The Society met in the rooms of the Linnean Society, Burlington House, London, on Tuesday, 21 March 1944, the President taking the chair at 10.30 a.m. Some sixty members and guests were present. The symposium centred about Gause's contention (1934) that two species with similar ecology cannot live together in the same place, and the bearing of this, if true, on the origin and persistence of species. A distinct cleavage of opinion revealed itself on the question of the validity of Gause's concept. Of the main speakers, Mr Lack, Mr Elton and Dr Varley supported the postulate. *Mr Lack* argued that, at least in birds, geographical isolation seems an essential precursor to species formation and that if, later, two geographical races meet they may be genetically intersterile and will inevitably compete, with varying results: (i) elimination of one by the other, (ii) elimination of one at the point of overlap, but its survival over parts of its range where it is the better adapted, and so geographical replacement, (iii) habitat replacement due to adaptation to different zones of the ancestral habitat, or (iv) co-survival resulting from divergence in food preferences. It is probably only those geographical forms which have acquired some degree of ecological differentiation which are capable of persisting in the same area should they later meet. He supported his argument by reference to three groups of passerine birds, namely Mayr's cases of passerines on remote islands, the British breeding species, and the finches of the Galapagos, and suggested that further examples were to be found among other animal groups.

Mr Elton presented an analysis of the species lists from some fifty ecological surveys of a variety of habitats. These showed a very high proportion of genera represented by single species. Figures culled from the literature on plant communities suggest similar species relationships among plants. Moreover when two species of a genus do occur together they often prove to be different ecotypes. There is also evidence, as, for example, the grey and red squirrels in Britain, that the introduction of an extra congeneric species from outside the community may only be successful at the expense of the native species. *Dr Varley*, accepting the Gausian concept, argued that the outcome of the competition between two closely allied species depends on the differences between them and on the severity of the different kinds of mortality. Mortality factors may be non-density dependent, e.g. the physical environment, or density dependent, i.e. competition for food and space, or destruction by predators or parasites. Together the mortality factors must destroy the surplus population. If other types of mortality are insufficient the population density will rise until some density dependent factor stabilizes the population density at a higher level. As mortality factors are the agents of Natural Selection, any change in the relative severity of their action will change the direction of evolution. The geographical replacement of closely allied species with similar food would be expected in continental areas, where physical factors or predators are predominant. In the absence of these factors two closely allied species will compete for the same food, and one will eliminate the other unless it will take food which the other rejects. Modified feeding habits will be favoured and will lead to adaptive radiation, as has happened among the cichlid fishes of the African Lakes (Worthington) and the Galapagos finches where predators are absent. In plants competitive factors may lead to pure communities, as in *Mesembryanthemum* and *Brachypodium pinnatum*. Co-dominance presents a difficult problem. In chalk pastures with many co-dominants the selective advantage for rapid growth may be balanced by selection by herbivores for stunted types.

Dr Blackman presented an analysis of Harland and Martini's experiments in which eleven varieties of barley were mixed and grown under a variety of conditions, random samples of the harvested grain being sown in successive seasons up to a maximum of eleven years. Finally, the numerical proportions showed marked changes, leading in various instances to suppression or dominance of one or other, or to co-dominance of two or more varieties. Arguing that varietal differences within a species may reflect inter-specific differences of ecological requirements—about which critical data are lacking—it was suggested that these results indicate that competition between two species of similar ecology may or may not result in the suppression of one by the other, the final balance depending on the conditions within the habitat.

Capt. Diver made a vigorous attack on Gause's concept, on the grounds that the mathematical and experimental approaches had been dangerously oversimplified and omitted consideration of many factors of which the importance varied among different organisms. These included sources of energy and their relative availability, predator attack, mobility, population structure and growth, individual growth-rate and bulk, relation of life cycle to annual cycle, range of tolerance, means of dispersal, and the like. Pointing out the difficulty of defining 'similar ecology' he gave examples of many congeneric species of both plants and animals apparently living and feeding together. He concluded that there was little direct evidence that co-habitation or separation of related species was determined by competition for space and food, since other factors usually kept populations below the point at which serious pressure was developed. *Mr Spooner* developed a similar argument, using examples from among the British wasps and bees, where populations are so restricted by the physical conditions that interspecific competition for either food or nesting sites rarely if ever becomes a limiting factor.

A lively discussion followed to which contributions were made by Mr Rose, Dr Butcher, Mr Lavender, Dr Thorpe, Miss Moore, Mr Goodall, Prof. Hale Carpenter, Prof. J. B. S. Haldane, Dr O. W. Richards, Dr Cragg, Dr Jones, Dr Uvarov, and Dr Clapham. The arguments pro and contra were fairly evenly balanced. Instances of mutually exclusive congeneric species included the *distans* section of *Carex*, the *pimpinelloides* section of *Oenanthe*, species of *Limonium*; while genera with species living together included *Drosera, Betula, Orchis, Ranunculus, Cimex, Drosophila, Pseudarcaea* (in Uganda), downland grasses, *Limnaea, Asellus* and others. Points made included: that in running water competition is characteristically between organism and physical environment rather than interspecific (Dr Butcher); that habitat preferences are often genetically fixed and may result in, and not from, geographical isolation (Dr Thorpe); while Prof. Haldane referred to the unseen competition of one species acting as a carrier of a parasite fatal to another, and to the need for research on the history of diseases of closely related species.

Those interested in the subject of the symposium may care to refer to two papers relating to it, which have been prepared by speakers who took part in the discussion. Mr Lack's paper has been published in the July number of *Ibis*, while Mr Elton's will be published in a forthcoming number of the *J. Animal Ecology*.

<div align="right">L. A. HARVEY</div>

BIOLOGICAL FLORA OF THE BRITISH ISLES

POLYGONUM L. em. Gaertn.

N. W. SIMMONDS

There are 14–16 British species grouped in four sections:

1. BISTORTA. Perennial, rhizomatous. Ocreae truncate. Raceme solitary. Stamens 8, styles 3, nut triquetrous. Basic chromosome number = 11. *P. bistorta* L., *P. viviparum* L.

2. PERSICARIA. Annual (*P. amphibium* is perennial). Leaves often with a blackish blotch, ocreae truncate. Racemes 1–many. Stamens 4–8, styles 2–3, nut trigonous or compressed. Basic chromosome numbers = 10 and 11. *P. amphibium* L., *P. lapathifolium* L., *P. petecticale* (Stokes) Druce (*P. maculatum* Trimen & Dyer, *P. nodosum* Pers. etc.), *P. persicaria* L., *P. hydropiper* L., *P. minus* Huds., *P. mite* Schk. (*P. laxiflorum* Weihe).

3. AVICULARIA (CENTINODE). Annual (*P. maritimum* is perennial). Ocreae silvery, bilobed. Flowers axillary, solitary or fascicled, stamens 8, styles 3, nut triquetrous. Basic chromosome number = 10. *P. aequale* Lindm., *P. heterophyllum* Lindm., *P. calcatum* Lindm., *P. raii* Bab., *P. maritimum* L.

4. TINIARIA. Annual, usually twining. Leaves cordate or sagittate, ocreae truncate. Flowers in racemose clusters, stamens 8, styles 3, nut triquetrous. Basic chromosome number = 10. *P. convolvulus* L., *P. dumetorum* L.

The following are recorded as naturalized aliens:

P. polystachyum Wallich. (Himalaya). (Sect. ACONOGONON Meisn.)

P. sagittatum L. (North America). (Sect. ECHINOCAULON Meisn.)

P. cuspidatum Sieb. & Zucc. (*P. sieboldii* De V.) (Japan) and *P. sachalinense* Schmidt (Sachalin). (Sect. PLEUROPTERUS B. & H.)

Most of the species are rather variable and some are plastic, e.g. *P. amphibium*, *P. lapathifolium* (Danser, 1921). The members of the sect. Persicaria, with the exception of *P. amphibium*, and the *aequale-heterophyllum-calcatum* complex (*P. aviculare* L.), are critical, and hybrids within these two groups are said to be frequent. The ocrea is a very characteristic vegetative feature.

Cytology. The basic chromosome numbers given in the synopsis of the sections above are taken from Jaretsky (1928, pp. 479–80). Polyploidy is frequent.

Habit. All the species are herbaceous, but habit and branching vary considerably, often within one species. *P. convolvulus* and *P. dumetorum* are twining plants; *P. bistorta* and *P. viviparum* have erect, unbranched stems. Members of the section Avicularia are generally more or less straggling and prostrate, though often with some ascending branches, while those of the section Persicaria are commonly erect and branched, though some species may be found unbranched or prostrate. In the latter case, adventitious roots may occur at the nodes; they may also occur where, as frequently happens, the base of an erect stem is procumbent.

Of the aliens, *P. cuspidatum*, *P. sachalinense* and *P. polystachyum* have tall, little-branched stems spreading by rhizomes, while *P. sagittatum* is a straggling annual.

Duration, life-form. *P. maritimum* is a hemicryptophyte, *P. bistorta* a rhizome hemi-cryptophyte, *P. viviparum* a geophyte and *P. amphibium* may be a hydrophyte or hemi-cryptophyte. The rest are annuals (therophytes), though *P. raii* may be biennial. Of the aliens, *P. sagittatum* is a therophyte and the rest are rhizome geophytes.

Flowers. The flowers are small, sessile or subsessile and massed in spike-like racemes (except in section Avicularia, where they are solitary or fascicled in the leaf axils). The perianth is red, pink, white or greenish; nectar may be secreted.

Pollination is by insects in the protandrous *P. bistorta*; entomophily may also occur in *P. persicaria* and *P. lapathifolium*, but automatic self-pollination occurs here by the incurving of certain stamens on to the stigma. The flowers of *P. minus* are more constantly selfed than those of the last two species, while self-pollination is habitual in *P. aviculare* agg. (Knuth, *Poll.* **3**, 341–9). It may be noted that *Fagopyrum esculentum* Moench (which has often been included in *Polygonum*) is heterostyled. Thus there is a considerable range of behaviour in respect of floral biology.

Ecology. Various. *P. raii* and *P. maritimum* are plants of the sea coast; *P. viviparum* is alpine; *P. bistorta* occurs in meadows, etc.; *P. amphibium* grows in or by ponds, ditches, etc., and the rest are plants of open habitats almost always associated with disturbance and cultivation. Members of the section Persicaria tend to occur in damp habitats.

Geographical distribution is, in general, through temperate and north Europe, Asia and America, though some of the weed species have spread greatly and become almost cosmopolitan in distribution.

REFERENCES

Danser, B. H. (1921). Contribution à la systématique du *Polygonum lapathifolium.* *Rec. trav. bot. néerl.* **18**, 125–210.

Jaretzky, R. (1928). Histologische und karyologische Studien an Polygonaceen. *Jb. wiss. Bot.* **69**, 357–490.

INSECTS AND FUNGI ASSOCIATED WITH *POLYGONUM*

INSECTS (O. W. RICHARDS)

Since a number of records do not distinguish the species of *Polygonum* and others suggest that many of the insects are attached to several, it has been thought best to deal with the genus as a whole. Only insects closely attached to *Polygonum* are included and continental records of the food habits of British insects have been used where necessary. Where no species of *Polygonum* is mentioned, the records refer to the genus; the species of *Polygonum* are abbreviated as follows: *P. amphibium* L., am.; *P. aviculare* L., av.; *P. bistorta* L., b.; *P. convolvulus* L., c.; *P. hydropiper* L., h.; *P. lapathifolium* L., l.; *P. petecticale* (Stokes) Druce (*P. nodosum* Pers., *P. maculatum* Trimen & Dyer, etc.), pc.; *P. persicaria* L., pr.

HEMIPTERA-HOMOPTERA

APHIDIDAE: *Capitophorus hippophaës* (Walk.), in winter on *Hippophaë rhamnoides*, in summer on *Polygonum* (h., l.). *C. gillettei* Theobald has the same habits as the preceding, from which it may not be distinct. *C. ribis* (L.), in winter on *Ribes*, in summer on various labiates (*Lamium*, *Galeopsis* and *Stachys*) and, according to some workers, *Polygonum* (pr., h., l). *Aspidaphis adjurans* (Walk.), on av. and *Lycopsis arvensis* (Laing, 1921). *Aphis* (*Doralis*) *neopolygoni* Theob. on *Polygonum* sp., pc. and on *Fagopyrum*. *Myzus polygoni* (Buckt.), pr.

PSYLLIDAE: *Aphalara calthae* (L.), av., am., h., and *Rumex acetosella*.

COLEOPTERA

CHRYSOMELIDAE: *Gastroidea viridula* (Deg.), and *G. polygoni* (L.) widespread on *Rumex* and *Polygonum*. *Chaetocnema concinna* (Marsh.), adult common and widespread, chiefly on *Polygonum*. *Mantura rustica* (L.), larva in blotch in leaves, *av.*

CURCULIONIDAE: *Rhinoncus perpendicularis* (Reich.), *am.*, local but widespread. *Rh. bruchoides* (Hbst.), England south to Lincs. *Rh. inconspectus* (Hbst.), widespread but very local. *Phytobius quadrinodosus* (Gyll.), *am.*, south England, rare. *Ph. quadricornis* (Gyll.), *l.*, widespread but rare. *Ph. waltoni* Boh., *h.*, south England, very local. *Apion difforme* Germ., south England to Norfolk, local, *pr.* (O.W.R.).

DIPTERA

CECIDOMYIDAE: *Dasyneura persicariae* (L.), *am.*, *pr.*, ? *av.*, larvae either deform flowers, or, more commonly, roll in the leaf margins which are reddened and swollen. *D. bistortae* (Kieff.), *b.*, *pr.* (Bagnall & Harrison, 1921).

MUSCIDAE: *Pegomyia nigritarsis* (Zett.) and *P. bicolor* (Wied.), larvae in blotch in leaf of *Rumex* and *Polygonum*, former chiefly on *Rumex*, latter chiefly on *Polygonum* (Hering, 1937). Both species are common, at least in south England. *P. setaria* (Meig.) mines leaves of *c.*, at least on Continent (Karl, 1928).

HYMENOPTERA

TENTHREDINIDAE: *Protemphytus perla* (Klug), *pr.*, apparently widespread. *Ametastegia equiseti* (Fallén), chiefly on Polygonaceae, *pr.* *A. glabrata* (Fallén), chiefly on Polygonaceae, *am.*, *b.*, *h.*, *pr.* The last two species are common, at least in England.

LEPIDOPTERA

NOCTUIDAE: *Hadena* (*Dipterygia*) *scabriuscula* (L.), *Polygonum* and *Rumex*, England, rare in the north.

HELIODINIDAE: *Augasma aeratellum* (Zell.), larva in galls among flowers or in distal parts of stem, petioles, etc., *av.*, *l.*, south-east England, local.

GRACILARIIDAE: *Gracilaria phasianipennella* (Hb.), *h.*, *pr.* and *Rumex*, rarely *Lysimachia* or *Lythrum*, larva at first in mine, then in rolled strips of leaves, widespread but local.

In preparing the above lists, valuable assistance has been given by Dr H. F. Barnes, Mr R. B. Benson, Mr W. E. China, Mr C. T. Gimingham and Dr G. D. Morison.

REFERENCES

Bagnall, R. S. & Harrison, J. W. H. (1921). New British Cecidomyidae. I. *Ent. Rec.* **33**, 151–5.
Hering, M. (1937). *Die Blatt-Minen Mittel- und Nord-Europas.* Lief. 4. Neu-Brandenburg.
Joy, N. H. (1932). *A Practical Handbook of British Beetles.* London.
Laing, F. (1921). On various genera of British Aphides. *Ent. Mon. Mag.* **57**, 118–27.
Also: **Edwards**, *Hem.-Hom.*; **Meyrick**, *Lepidopt.*; **Theobald**, *Aphid.* **1** and **2**.

NEMATODES (A. SMITH)

It has proved impossible to disentangle British records from World host records.

Anguillulina dipsaci (Kühn) Gerv. & V. Ben. has been recorded on *P. aviculare*, *P. convolvulus*, *P. lapathifolium*, *P. persicaria*. *Anguillulina pratensis* (de Man) Goffart has been noted on *P. aviculare*, *Heterodera schachtii* Schmidt on *P. aviculare* and *P. lapathifolium*. These and the preceding are British records. *Heterodera marioni* (Cornu) Goodey

has also been recorded on various species but presumably in warmer countries, though it might appear on greenhouse weeds in the British Isles.

Dr O. W. Richards gives the following record: *Tylenchus devastatrix* Kühn. on *P. convolvulus*, causing a shortening and thickening of internodes, swelling and torsion of stem and often hypertrophy of leaves. (Houard, **1**, 385.)

<div align="center">FUNGI (A. SMITH)</div>

PHYCOMYCETES

PERONOSPORALES: *Peronospora polygoni* Thüm. on *P. convolvulus* and *P. aviculare*.

ASCOMYCETES

PEZIZALES: *Phialea scutula* Gill, var. *fucata* Phill. on *Polygonum* sp.

ERYSIPHALES: *Erysiphe polygoni* DC. occurs on many hosts but is abundant on *P. aviculare*.

SPHAERIALES: *Gnomoniella devexa* Sacc. on *Polygonum* sp. *Ceriosporella polygoni* A. L. Sm. & Ramsb. on *Polygonum* sp. *Stigmatea polygonorum* (Fr.) Fr. on *Polygonum* sp.

BASIDIOMYCETES

USTILAGINALES: *Sphacelotheca hydropiperis* (Schum.) de Bary on *P. hydropiper* and other spp. *Ustilago bistortarum* (DC.) Koern. on *P. bistorta* and *P. viviparum*. A specimen of this last fungus on *P. petecticale*, Simmonds states, is in the Marshall Herbarium in the Botany School, Cambridge. Plowright gives as hosts *P. lapathifolium*, *P. persicaria*, *P. convolvulus* and *P. hydropiper* and Massee adds *P. aviculare*. It is uncertain, however, how far these records apply to material of British origin. It was recorded in Norfolk on *P. hydropiper* in 1934.

UREDINALES: *Uromyces polygoni-avicularis* (Pers.) Ramsb. on *P. aviculare*. *Puccinia polygoni-amphibii* Pers. on *P. lapathifolium* and *P. amphibium*. *Puccinia polygoni-convolvuli* DC. on *P. convolvulus*. *Puccinia conopodii-bistortae* Kleb. on *P. bistorta*. *Puccinia polygoni-vivipari* Karst. on *P. viviparum*. *Puccinia septentrionalis* Juel. on *P. viviparum* and by inoculation on to *P. bistorta*.

FUNGI IMPERFECTI

HYPHOMYCETES: *Ovularia bistortae* (Fuckel) Sacc. on *P. bistorta*. *Bostrichonema alpestre* Ces. on *Polygonum* sp.

COELOMYCETES: *Phyllosticta polygonorum* Sacc. on *P. persicaria*. *Phoma polygonorum* Cooke on *P. cuspidatum*. *Phomopsis polygonorum* Grove on *P. baldschuanicum* and *P. cuspidatum*. *Cytospora polygoni-sieboldii* Henn. on *P. sachalinense*. *Amphorula sachalinensis* Grove on *P. sachalinense*. *Septoria polygonorum* Desm. var. *persicariae* Trial and *S. polygonicola* Sacc. do not appear to be more than variants. *Myxosporium polygoni* Grove on *P. sachalinense*.

Few of the above fungi appear to have any ecological significance. *Sphacelotheca hydropiperis* can frequently render patches of *P. hydropiper* almost entirely sterile; the plant, however, appears to be as frequent as ever in the following season. On *P. persicaria* as a field weed, *Septoria polygonorum* may cause a good deal of premature leaf-scorching, which however does not appear to cripple the host.

The above list has been compiled from the usual sources (see *J. Ecol.* **32**, 117, 1944), together with:

Wilson, M. (1934). The distribution of the Uredineae in Scotland. *Trans. Bot. Soc. Edinb.* **31**, 345–449.

Polygonum persicaria L.

N. W. SIMMONDS

Sect. PERSICARIA. Stem erect, ascending, decumbent or prostrate, sometimes rooting at the lower nodes, branched or not, 3–80, usually about 30 cm. in height. Nodes swollen or not, often with a red sub-ocreal ring. Ocreae tight, with appressed hairs, the margins ciliate. Leaves very variable in size and shape, usually blotched with brownish red and petioled, the surfaces with scattered hairs, not tomentose. Inflorescences 1 to many, the peduncles glabrous or hairy, rarely with a few glands. Racemes dense, very variable in size and shape. Perianth red or pink, rarely white, glabrous or with a few glands. Styles 2 or 3, united to half way. Fruit blackish brown, trigonous or compressed, but not biconcave, about 2·5 × 2·0 mm., equal to or longer than the perianth.

An extremely variable species best characterized by the generally abundant pigmentation, tight ciliate ocreae, united styles and especially the shape of the nut (Fig. 1). Many varieties have been described; see Britton (1933); Aschers. & Graebn. **4**, p. 815, etc.

Fig. 1. Typical fruits of *P. lapathifolium* L. (A), *P. petecticale* (Stokes) Druce (B), and *P. persicaria* L. (C). All × 15. The dotted line represents the position of the perianth.

Many of these varieties no doubt have a genetic basis, but none appears to be distinct, and plants are often found which defy classification. Experimental study of the plasticity of the species is much needed. Britton (1933) recognizes the var. *elatum* Gren. & Godr. (characterized by the long, slender inflorescences), var. *agreste* Meisn., and the prostrate varieties *ruderale* Meisn. and *prostratum* Bréb. Moss (1914, pp. 115-16) recognizes the vars. *agreste* and *ruderale* and there are numerous others, none of certainly known status. The situation is probably similar to that in *P. lapathifolium* (q.v.), in which there appears to be a wealth of genetic variability of a kind which does not lend itself to taxonomic treatment, accompanied by plasticity.

A native of Europe, widely distributed as a weed of cultivation and a common plant of arable land, ditches, roadsides and numerous other disturbed communities throughout Britain.

I. *Geographical and altitudinal distribution.* Recorded for all English and Irish vice-Counties.

Throughout Europe to 70° N. in Norway (Blytt, 1906, p. 288), to 60° 30′ N. in Finland (Hermann, 1912, p. 159), 63° 40′ N. in Sweden (Lindmann, 1926, p. 239) and 60° 30′ N. in Ladoga-Ilmen, European Russia (Komarov, 1936, p. 652). East to Central Russia, North India, Japan, Australia and New Zealand. Also in Asia Minor, the Caucasus, Transcaucasia, Syria, Palestine, and North Africa from Egypt to Morocco. 'In waste places throughout temperate and tropical North and South America' (Small, 1913, p. 378).

Introduced in America, Australia, New Zealand and probably elsewhere. In Australia, unrecorded by Bentham (1870) (cf. *P. lapathifolium*); the first record appears to be for Victoria in 1908 (Ewart, 1930, p. 431). In New Zealand, first recorded at Wellington in 1877 (Thomson, 1922, p. 465).

Ascends to 1420 ft. (432 m.) in Cardigan (Salter, 1935, p. 126), to 1350 ft. (411 m.) in Aberdeen, Derby and Cumberland, to 1250 ft. (380 m.) in Dublin and Kerry (Alt. Range Br. Pl.); probably to the upper limits of cultivation. In western Tibet, Hooker
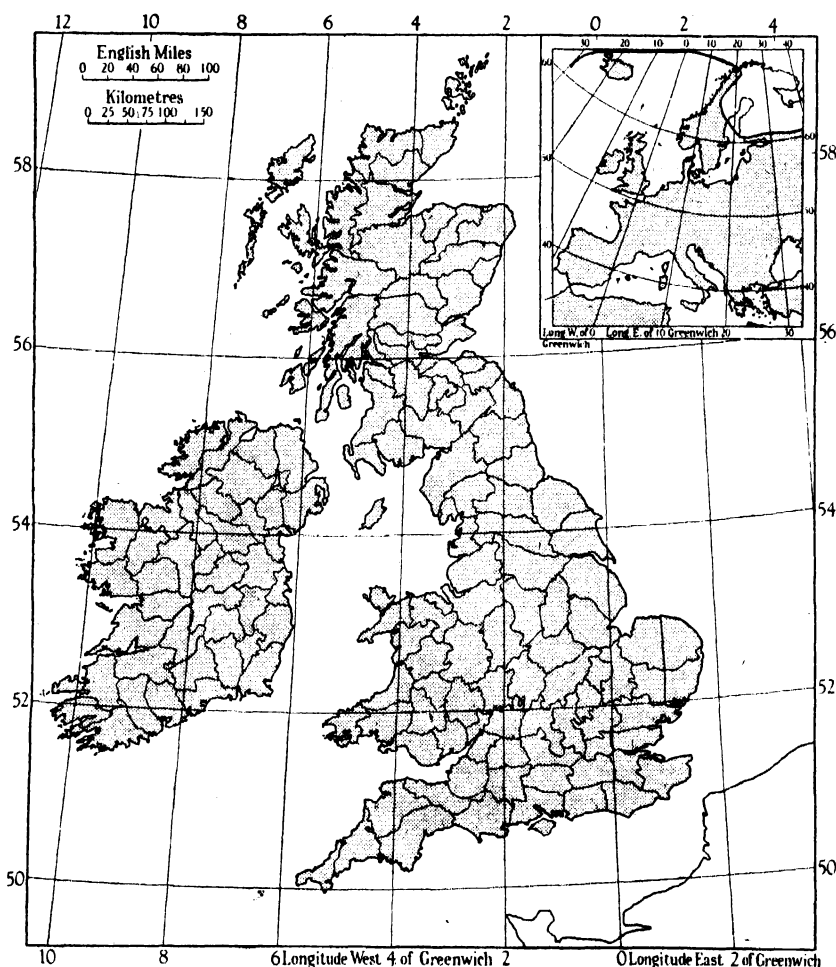
Fig. 2. *Polygonum persicaria* L.: vice-comital distribution in the British Isles and (inset) distribution in Europe.

(1890) records it up to 14,000 ft. (4260 m.) while in Europe it ascends to 5910 ft. (1800 m.) in Graubünden (Braun-Blanquet & Rübel, 1933, p. 449) and to 5350 ft. (1630 m.) in the north Tirol (Hegi *Fl.* 3, p. 201).

II. *Habitat.* Always in disturbed communities such as waste ground, arable land, ditches, roadsides, etc. On the Somme battlefields of 1914–18 war after shelling had churned up the ground, often in standing water in shell-holes (Hill, 1917). An important weed of arable land, often in rather damp situations.

On a wide variety of soils. As an arable weed it is rare on chalk but otherwise shows no very marked soil preferences. In East Anglia appears to avoid heavy clays, but

Brenchley (1920, p. 133) records it as indifferent in Bedfordshire and says that it may be very abundant on such soils in Somerset. The following table (Table 1) is taken from Brenchley (1920, p. 131) and is a summary of a survey carried out in Bedfordshire, Wiltshire, Somerset and Norfolk (cf. Brenchley, 1911, 1912, 1913 and see also III, below).

Table 1. *Percentage occurrence of* Polygonum persicaria *L. on various soils*
From Brenchley, 1920, p. 131

	Percentage occurrence on				
All soils	Heavy	Medium	Light	Chalk	Peat
12	2·6	12	13	0·6	90

Brenchley (1920, p. 133) states that it may be aggregated in the wetter parts of a field and suggests that its rareness on chalk is due to its relatively high water requirements, also (p. 155) that it is a very common weed of wet, acid peat land in Nottinghamshire.
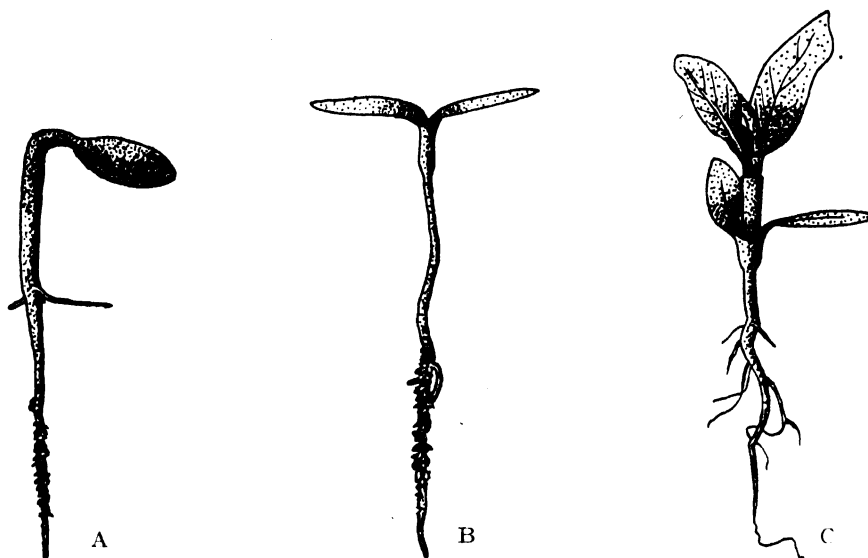
Fig. 3. Seedlings of *P. persicaria* L. A, × 6; B, × 4·5; C, × 2.

Buchli (1936), working in the 'Dreifeldwirtschaftgebiet' of Switzerland, concluded that *P. persicaria* tends to occur on the base-rich soils, but, when tested statistically, his data give no evidence of soil preference in respect of: (a) $CaCO_3$ in the range 0–55 %, (b) pH in the range 6·5–9·0, (c) clay content in the range 7·5–62·5 % and (d) sand content (particles over 2 mm. diam.) in the range 0–62·5 %. His sampling unit appears to have been the field, so that there is always the possibility that, *P. persicaria* depending on local conditions within a field, his samples do not give a true picture of the soils on which it grows.

In Cambridgeshire it has been seen on black fen peat (pH 6·9 at the surface (colorimetric)) (though less common as a weed there than *P. lapathifolium*), on a silty river alluvium (pH 7·2 (colorimetric)) at Coe Fen, on the mud banks of Wicken Lode, on heavy boulder-clay (though rarely only) at the University Farm.

Also seen on chalky boulder-clay in a chalk pit at Foxhole heath in the Suffolk Breckland, on sand at Dersingham, Norfolk (pH 6·6–6·9 (colorimetric)), at Barton Mills, Suffolk (pH 7·5 (colorimetric)) and frequently in east Dorset (acid); on heath peat over-

lying a sandy podsol at West Moors, Dorset. It occurs also on river mud at Coe Fen, Cambridge, and on cinders and manure heaps. Salisbury (1921, p. 365) records it on dried mud exposed at the bottom of the Welsh Harp Reservoir, Middlesex (see VIII (*j*), below).

Evidently extremely tolerant of a wide range of edaphic conditions; its occurrence is probably determined chiefly by disturbance and consequent reduction in competition.

III. *Communities.* As an arable weed, it is rarely found in grass or clover (seeds), but is not otherwise associated with any particular crop, according to Brenchley (1920, p. 169) (Table 2). The rarity in seed crops is probably the result of their dense growth and hence greater competition. Note however (VIII (*h*)) that the fruits are fairly frequently present in samples of red clover seed. These data at least prove the occasional presence of the weed in the crop concerned, but give no further ecological information except in the case of flax, in which the three weed 'seeds' most constantly present, and often associated, were *Atriplex patula, Chenopodium album* and *P. persicaria.*

Table 2. *Occurrence percentage of* Polygonum persicaria *L. in various crops*
(From Brenchley, 1920, p. 169.) (Seen in all 132 times)

			Percentage occurrence in			
All crops	Wheat	Barley	Oats	Roots	Peas, Beans	Seeds
12	10	12	18	15	10	3

The following contingency table has been constructed from the data of Buchli (1936, p. 97):

Table 3. *The distribution of* P. persicaria *L. in corn crops in Switzerland*
(From Buchli, 1936)

	Present	Absent	Total
Winter barley	2⎱ 10	36⎱ 119	38⎱ 129
Winter rye	8⎰	83⎰	91⎰
Winter wheat	35	78	113
Winter corn total	45	197	242
Spring corn	7	22	29
Total	52	219	271

Combining the figures for barley and rye on account of the small number of the former, we have $\chi^2 = 21 \cdot 462$ ($n = 2$, p very small) for a comparison of winter barley and rye with winter wheat and spring corn. If the figures for winter crops are combined we have $\chi^2 = 0 \cdot 516$ ($n = 1$, $p = 0 \cdot 3 – 0 \cdot 5$) for a general comparison of spring and winter corn. Thus the significant heterogeneity shown by the first test is due to the differential effect of barley and rye as against wheat. No full explanation of this association with winter wheat is possible, but it is probably related to the rotational system in force in that part of Switzerland (cf. Buchli, 1936, p. 9 et seq.). Broadly, this is Winter Wheat followed by another corn crop followed by potatoes or clover, i.e. *P. persicaria* tends to occur in the first of two corn crops and follows potatoes or clover. The data are too limited to carry the analysis any further, but this seems on the whole a more probable relation than that it tends to occur in winter wheat as such.

There is a considerable variety of associated species. The lists following are samples. 1 and 2 were more or less closed communities liable to periodic disturbance by livestock, ditch-cleaning operations, etc.; the rest were all open communities.

(1) On a ditch bank at Coe Fen, Cambridge. *Polygonum hydropiper, Poa pratensis,*

Taraxacum sp., *Plantago major, Urtica dioica, Trifolium pratense, Atriplex* sp., *Dactylis glomerata, Rumex acetosa, Lolium perenne, Sonchus asper.*

(2) A different locality on Coe Fen. *Polygonum hydropiper, P. aviculare, Rumex conglomeratus, Ranunculus repens, Festuca pratensis, Lolium perenne, Urtica dioica, Agrostis* sp., *Stellaria* sp., *Cirsium arvense.*

(3) In a bean crop at Dersingham, Norfolk. *Polygonum lapathifolium, P. petecticale, Urtica dioica, Anagallis arvensis, Cirsium lanceolatum, Holcus mollis, Chenopodium album.*

(4) On a ditch bank near West Moors, Dorset. *Polygonum hydropiper, Urtica dioica, Rumex conglomeratus, Holcus mollis, Geranium* sp., *Potentilla anserina, Heracleum sphondylium, Bidens tripartita, Dactylis glomerata, Poa trivialis, Solanum dulcamara.*

(5) On a sand and gravel bank thrown up from a ditch in a *Molinia-Myrica-Juncus* community at West Moors, Dorset. *Holcus lanatus,* f., *Rumex acetosella,* f., *Agrostis* sp., o., *Molinia caerulea,* o., *Rubus* spp., o., *Polygonum persicaria,* o., *P. lapathifolium,* r., *Juncus effusus,* r., *P. hydropiper,* r., *Atriplex* sp., r., *Anthoxanthum odoratum,* r.

(6) In a damp rut in a sandy heath track, Grange estate, near West Moors, Dorset. *Polygonum persicaria,* a., *Matricaria matricarioides,* a., *Sagina apetala,* a., *Juncus bufonius,* a., *Poa annua,* f., *Gnaphalium uliginosum,* f., *Agrostis* sp., o., *Plantago major,* o., *Polygonum aviculare,* o., *Cerastium triviale,* o., *Poa trivialis,* r., *Trifolium repens,* r., *Sonchus* sp., r., *Capsella bursa-pastoris,* v.r., *Rorippa islandica (Nasturtium palustre),* v.r., grass and other unidentified seedlings f.

(7) A ditch, Horton Heath, Dorset. *Polygonum hydropiper,* a., *Potentilla anserina,* a., *Ranunculus acris,* o., *Lolium perenne,* o., *Polygonum aviculare,* o., *P. persicaria,* o., *Filipendula ulmaria,* o., *Rumex conglomeratus,* o., *Lycopus europaeus,* r., *Poa trivialis,* r., *Achillea millefolium,* r.

(8) Long (1938, p. 2) gives the following list of seedling weeds for a square yard of garden soil: *Ranunculus* (chiefly *repens*), *Poa annua, Rumex* sp., *Chenopodium album, Senecio vulgaris, Capsella bursa-pastoris, Sonchus oleraceus, Stellaria media, Polygonum persicaria, Sinapis arvensis, Cirsium arvense, Plantago* sp., *Trifolium* sp.

Characteristic of the *Polygonum hydropiper* communities frequent in wet ditches in the east Dorset-west Hants region. These are closed communities (at least in summer), often in standing water and are sometimes shaded by trees (cf. below).

Braun-Blanquet and Rübel (1933, **2**, p. 449) record it as a member of the *Chenopodium polyspermum-Panicum crus-galli* association in Graubünden, while Hegi (*Fl.* **3**, p. 202) gives the following list of characteristic associates in central Europe: *Equisetum arvense, Polygonum convolvulus, Amaranthus retroflexus, Solanum nigrum, Linaria vulgaris, Capsella bursa-pastoris, Galium aparine, Sonchus arvensis, S. oleraceus, Senecio vulgaris, Cirsium arvense, Vicia hirsuta, Stellaria media, Veronica agrestis, Euphorbia helioscopia.*

In general occurs in open, sometimes intermittent habitats and is associated with a wide range of other weed spp. Perhaps more tolerant of competition in wet situations; cf. the closed *P. hydropiper* communities in wet ditches in Dorset.

IV. *Response to biotic factors.* Not often grazed and has been said to be poisonous to stock. Long (1910, p. 114) however states that it is useful fodder for horses and cattle. At Coe Fen, Cambridge, a variety approaching the var. *prostratum* withstands grazing and trampling by cattle and horses. This variety, together with other prostrate types characteristic of paths, cart-ruts, etc., may be forms of trodden habitats. Abundant in a potato field in Bedfordshire (1942) where there occurred a gradation of forms from erect

on the field itself to prostrate on an adjoining path (R. M. Greenslade). Experiment on these prostrate forms is needed.

Druce (1897, p. 427) says: 'When growing on goose-greens where the plant is much bitten off, it assumes something of the appearance of *Polygonum minus.*'

If cut back, even when in full flower, it may persist into a second year (J. Carpenter).

Long (1938, pp. 172–3) states that hoeing and hand-pulling are the best methods of controlling it as a weed and that 4 % copper sulphate and 7–10 % sulphuric acid are effective as sprays, the latter in cereal crops.

V. (*a*) *Gregariousness.* Sometimes solitary, usually a number of plants together, or in dense stands. Aggregation of seedlings, presumably on the site on which the seed-parent of the previous year had grown, has been noted at Hampreston, Dorset (D. Trehane).

(*b*) *Performance in various habitats.* Some, at least, of the great variability of this species is due to plasticity. There are many references in the literature to certain varieties being 'mere forms' of dry habitats, poor soils, etc. Moss (1914, p. 116) suggests that the var. *ruderale* is a form of dry habitats (cf. IV above, where it was suggested that prostrate forms may be induced by treading). Drabble (1916) records 'paedogenetic plants about 1 inch high and with a few (3 or more) flowers' in Derbyshire. In the community listed in III (6), above, the species was represented by numerous, small plants, 3–15 cm. high, erect, unbranched, or branched once from the base and bearing from 3–30 flowers in one or very few racemes. The most depauperate plants occurred in what appeared to be the driest situations on mobile sand by the edge of the rut itself.

Habit appears to be affected by crowding; solitary plants are often branched from the base, the branches spreading and ascending. When densely crowded (e.g. at Gamlingay, Cambs., 1942), may form a close stand of tall, slender stems, 60–80 cm. high, little or not branched, the lowermost 20–40 cm. bare of green leaves and generally pale in colour. Nuts of *P. persicaria* (growing in a mixed stand with *P. lapathifolium* in which both species showed this 'crowded form') were sown in a pot and produced a single plant, strongly pigmented and branched from the base, the branches spreading and ascending.

Hegi (*Fl.* 3, p. 202) records 'second generation' plants, small and flowering only very little. It is not clear whether he regards the small size, etc. as in some way a consequence of late germination. If it were, this might explain some at least of the depauperate plants encountered as in III (6) above, and at Wicken Fen, Cambs. The latter occurred on the newly made mud banks of the lode and were slender, usually unbranched, erect or creeping, with a few small leaves and a few small inflorescences. *P. lapathifolium* and *P. petecticale* were similarly represented. The possible mode of action of late germination in producing these forms is, however, quite unknown.

(*c*) *Effect of frost, drought, etc.* No information.

VI. (*a*), (*b*) *Morphology, etc.* Underground part generally consists of roots only, but up to 5 cm. of stem may be buried, producing whorls of roots at the nodes (cf. root production at the nodes of procumbent overground branches). Main root generally rather contorted, but growing roughly vertically downwards unless the plant is growing on the side of a clod, etc.; from 3 cm. in length in small plants to about 20 cm., usually 10–12 cm. Rarely, a lateral may become the longest and stoutest root.

(*c*) *Mycorrhiza.* Chiovenda (1920) states that, in Italy, the rare fungus *Myriostoma coliliforme* (Dichs.) Corda (which is recorded as rare in Britain) was responsible for an endotrophic mycorrhiza in the roots of *P. persicaria.*

(d) *Perennation.* Summer annual (therophyte). See IV, however.

(e) *Vegetative reproduction.* Not known to occur.

(f) *Longevity.* One season only. Seedlings appeared in early April 1943 on Coe Fen, Cambridge, and mature plants were dead by late November 1942 in the same locality, i.e. the longevity is about 8 months, or less for plants germinating later in the season. Exceptionally, survives into a second season (see IV).

(g) *Age at first flowering.* About 6 weeks on Coe Fen, Cambridge, 1943. Nearly 2 months in pot tests, 1944.

(h) *Frequency of seed production.* Every year, so far as is known.

(i) *Ecotypes.* No information.

(j) *Chromosome number.* A tetraploid with somatic number 44 and 22 bivalents at meiosis (Jaretsky, 1928, p. 417). Somatic count tentatively confirmed on root tips of British material.

Pollen grains larger than those of the diploid *P. lapathifolium*; 10 had a mean diameter of $41 \cdot 6\ \mu$ (S.E.M. 0·72) and a mean volume of $51,400\ \mu^3$ (about 1·65 times that of *P. lapathifolium*).

Very few pollen mother cells (Jaretsky, 1927) are produced and pollen production is low. A very few pollen grains have been seen to have germinated within the anthers (see *P. lapathifolium*).

VII. *Phenology.* (a) Time of maximum root growth not known.

(b) Flowers from May–June to September or even later.

(c) Fruits shed from June or July onwards.

(d) Non-flowering shoots have not been seen. Short axillary or basal shoots (the flowers of which are often very pale in colour) may be produced from about June onwards.

(e) Seedlings first seen in early April on Coe Fen (1943), but not until mid-May 1944. An examination of the temperature and rainfall records made at the Cambridge Botanic Gardens near by did not reveal any obvious reason for this difference. Young seedlings were also seen on 17 July 1944 in the community listed under III (6) above, and germination (first or second generation?) probably occurs even later than this. Generally, however, a spring germinator, as noted by Buchli (1936, p. 273) in Switzerland, who also found a few seedlings during the winter.

VIII. (a) *Mode of pollination.* Knuth (*Poll.* 3, p. 346) says: 'Insect visits are fairly frequent; cross-pollination is therefore possible though automatic self-pollination often takes place.' The outer whorl of 5 stamens bends outwards and dehisces introrsely while the inner whorl of 1, 2 or 3 stamens, when present, bends in towards the stigmas and dehisces extrorsely, thus procuring self-pollination; this is said to occur, however, even when the inner whorl of stamens is lacking. Stigmas and stamens stand at roughly the same level and development is homogamous. Very little nectar is produced.

(b) *Insect visitors.* In Westphalia, Knuth (*Poll.* 3, p. 346) records Syrphides as the commonest visitors. In Britain, Scott-Elliot (1896, p. 150) gives *Bucentes (Siphona) cristata* (Fab.) (Tachinidae) and *Phaonia (Hyetodesia) incana* (Wied.) (Muscidae) and Dr Morison has found *Taeniothrips atratus* (Hal.) and *T. vulgatissimus* (Hal.) on this species.

(c) *Cleistogamy.* Not recorded, but the occasional pollen grains germinated within the anthers are suggestive (see *P. lapathifolium*).

(d) *Apomixis.* Not recorded.

(e) *Vivipary.* Not recorded.

(*f*) *Hybrids*. A number of hybrids have been claimed on taxonomic grounds, but the variability of most of the species concerned probably renders such identification uncertain. Britton (1929, 1930, 1933, 1935, 1936) has recorded hybrids with the following: *P. mite, P. lapathifolium, P. minus* (= *P. braunianum* Schultz), and *P. hydropiper* L. Specimens named × *P. hydropiper* L. and × *P. maculatum* Trimen & Dyer exist in the Cambridge University Herbarium and Aschers. & Graebn. (4, p. 820) mention hybrid with *P. lapathifolium* (as *P. tomentosum* Schr.), *P. petecticale* (as *P. nodosum* Pers.), *P. hydropiper, P. minus* and *P. mite*. Druce (1892, 1930) gives × *P. mite* and × *P. minus*.

The hybrid with *P. minus* (Britton, 1936) is said to be sterile, but generally there is no mention of reduced fertility and the specimens the writer has seen bear abundant well-formed fruits. The hybrids with the diploid species, *P. lapathifolium* and *P. petecticale*, would presumably be triploids and highly infertile, assuming that apomixis does not occur. The same applies to the × *P. hydropiper* with the addition that this species has a somatic chromosome number of 20, i.e. it has a different basic number (Jaretsky, 1928). The chromosomes of other species mentioned above are, as yet, uncounted. There is no information about ecological behaviour of hybrids.

(*g*) *Amount of seed*. 1 seed per fruit. From 3 per plant to about 1200 at one time; total throughout the season must usually be rather greater. Korsmo (1934) gives 200–800 nuts per plant.

Fruit weight: four samples of 25 nuts weighed respectively 59·8, 53·5, 56·4 and 62·3 mg. giving a mean of 2·3 mg. per fruit. Korsmo (1934) gives 2·7 mg. and Pammel (1910, p. 28) 1·41 mg.

(*h*) *Dispersal*. By animals. The following data are quoted by Ridley (*Disp. Plts.*). Heinitz in Sweden showed that the nuts could be eaten and passed through the intestines of horses (p. 360), cattle (p. 361), fallow and roe deer (p. 372) without harm. Several birds have been seen to eat the nuts; Holmboe quotes *Lullula arborea* (L.) (Woodlark) (p. 465) in Scandinavia and *Syrrhaptes paradoxus* (Pall.) (Pallas' Sand-grouse), a Russian steppe species occasionally migrating westwards in large numbers as far as Britain (p. 505). Beal records *Planesticus migratorius* (L.) (American Robin) (p. 477) and *Colaptes auratus* (L.) (Flicker) (p. 484) in America and Marrot found that *Anas strepera* L. (Gadwall), which is widely migratory over the temperate zone, also ate the fruits (p. 492). Evershed (1918) found fruits in the crops of pheasants. Praeger (*Ir. Top. Bot.* p. xxxviii) suggested that the fruits had been carried to a black-headed gull colony in King's County, Ireland, in mud on the birds' feet, and Brenchley (1920, p. 17) says that they may be distributed by sticking to clothes, animals, etc. when wet.

With agricultural seeds: given by Long (1910, p. 369) in Britain and by Pammel (1910, p. 33) in the U.S.A. as impurities in seeds, especially clovers. The records of the Official Seed-Testing Station, Cambridge, for the season 1942–3 were examined and yielded the following figures (given as percentage of samples tested containing fruits of the species): 0–1 %: *Trifolium hybridum, T. repens, Medicago lupulina, Onobrychis sativa, Lolium perenne, L. italicum, Dactylis glomerata, Phleum pratense, Cynosurus cristatus, Festuca* spp., *Brassica oleracea, B. rapa, Beta vulgaris, Peucedanum sativum*; 1–4 %: *Medicago sativa, Daucus carota*; 4–6 %: *Trifolium pratense, Festuca pratensis*; 31 %: *Linum usitatissimum*.

Briefly, the following factors are involved: (1) presence of the weed in the crop, itself, at least in part, dependent on the presence of the nuts in the crop seed; (2) relative

time of maturity of crop and weed; (3) seed size and weight in relation to cleaning processes; (4) harvesting methods. These are far too complex to discuss here, but the following points are of note: (1) the high figure for flax is probably less important than the 4·2 % for red clover, a much more widely grown crop; (2) there is a big international trade in seed and this must be an important means of world spread. Thus a high proportion of legume and grass samples were of foreign, especially American and New Zealand, origin; all the 6 % of records for *Festuca pratensis* came from the U.S.A. and some of the red clover records came from the U.S.A., Argentine, and New Zealand; (3) *P. lapathifolium* does not occur in any of the records seen and it is possible that it has not been distinguished from *P. persicaria*.

Volkart (1924) and Gentner (1929) have reported on the impurities of red clover samples from many European localities. From their combined data, it appears that the general mean number of nuts of *P. persicaria* per 1000 seeds of clover is about 6. Knowing the average seed-weight and seeding rates for red clover, it can be calculated that about 21,000 nuts will be sown per acre in pure red clover and about 6000 in mixtures; this is equivalent to about 5 and 1·5 fruits per sq. m. respectively. These figures are necessarily very approximate but they serve to illustrate the importance of agricultural seeds as a means of spread.

By water: Praeger (1913) showed that the nuts floated for one day, so that water-dispersal may occur.

(*i*) *Viability.* See (*j*).

(*j*) *Conditions for germination.* Justice (1941) showed that a period of after-ripening is necessary which is markedly shortened by subjecting the saturated fruits to low temperatures for a period of months, neither saturation nor low temperatures alone being efficient. After-ripening of the dry fruits does, however, occur slowly at ordinary temperatures, though the available figures show wide variation. Thus Justice obtained a maximum of 12 % after 30 months' storage and Ewart (1908) obtained 0 % after 1 year. The writer has obtained 8 % in light and 2 % in dark in laboratory tests on 50 nuts 11 months after harvest and 80 % in compost pot tests after 1 year's storage.

Prolonged dry storage, however, appears to lead to a decrease in viability; thus Dorph-Petersen (1924) records the following germination figures for 1–7 years' storage: 78, 63, 50, 13, 7, 2, 0 % respectively.

Justice (*loc. cit.*) showed that constant temperatures slightly above freezing (as against alternating temperatures) were most favourable to after-ripening, nuts thus after-ripened relapsing into secondary dormancy if dried. He also showed that outdoor burial in soil in winter was effective. Different media (e.g. paper, moss, cotton, etc.) were all shown to retard after-ripening compared with water, the suggestion being that they affected gaseous exchange in some way. This is consistent with the hastening of after-ripening found to result from the removal of the pericarp, e.g. intact nuts 4 months after harvest gave 4 % germination while a similar sample from which the pericarp had been removed gave 20 %. This question of gaseous exchange is probably important for nuts buried in soil, in which they are viable for long periods. Thus, according to Stapledon (1942) the period of viability under Welsh hill pasture was about 5 years and almost certainly less than 20 while periods of over 30 years have been found in Middlesex. Goss (1924), continuing the experiments of Duvel (1905), obtained the following data on the viability of fruits buried in 1902 at different depths:

Table 4. *Viability of the fruits of* Polygonum persicaria L. *in soil.*
(From Goss, 1924)

Depth of burial	Percentage germination in					
	1903	1905	1908	1912	1918	1923
8 in.	0	26	0	60·5	14	1
22 in.	0	1	0	31·5	9	25·5
42 in.	0	0	0	8	0·5	55

These figures are rather irregular but there is some indication that germination is delayed progressively at greater depths.

Appeared in abundance at Hampreston, Dorset, on land ploughed up for the first time in about 45 years (D. Trehane). Buchli (1936, p. 243) states that the nuts were viable after 20 years' burial and gives data on their occurrence in arable soils in Switzerland (pp. 221, 227). Salisbury (1921, p. 365) records it on dried mud at the Welsh Harp Reservoir, Middlesex, and it has been seen on mud newly exposed from a ditch on Coe Fen, Cambridge; nuts were probably present in the mud before exposure and drying in both these cases.

It appears therefore that low winter soil temperatures and saturation are the factors conditioning the spring-germinating habit of this species, while gaseous exchange may be limiting for after-ripening in the case of nuts deeply buried in soil or mud (cf. the probable effect of depth of burial in Table 4). It may be also that the generally higher temperatures with increasing depth in soil in winter are partly responsible.

(*k*) *Morphology of seedlings.* Woodcock (1914) has described the anatomy, etc. of the fruit. Germination occurs in 10–12 days. Nut splits at apex and radicle appears. Hypocotyl elongates and carries up the remains of the nut, later lost as the cotyledons expand. The region just below the cotyledons is at first a pale red, later turning green. Cotyledons orange-red in colour when first exposed, becoming dark green above and red below when expanded; they remain red in the dark. The ciliate ocrea can readily be seen at the base of the first foliage leaf. Distinguished from seedlings of *P. lapathifolium* and *P. petecticale* by the lack of glands and tomentum.

(*l*) *Effective reproduction.* Entirely by seed.

IX. *Parasites, diseases.* See *Polygonum* L. Virus: given by Smith (1937, p. 25) as a weed host of Beta Virus 1 (curly-top), in America.

X. *History.* Fossil records: Reid (1899, p. 139) gives records of the nuts in the Cromer Forest Bed of Suffolk, Interglacial of Sussex and London, late Glacial of Middlesex and Neolithic lacustrine deposits of the Scottish lowlands. Nuts possibly belonging to this species have been found in Mesolithic deposits in the Isle of Wight by Clifford (1936).

Regarded by Buchli (1936, p. 90) as an 'archaeophyte', i.e. a species having no known 'natural' habitat, always associated with human disturbance. (Note Reid's Pliocene record however.) The question of the earlier history of such archaeophytes presents many problems. Salisbury (1932, p. 193) has suggested that their natural habitats were for the most part early stages in succession where competition is comparatively low. Species that are now common weeds might then have been rare plants, colonizers of open or intermittent habitats. *P. persicaria* may then have occurred on the margins of lowland ponds and rivers, though, it must be emphasized, this is mere conjecture.

REFERENCES

Bentham, G. (**1870**). *Flora Australiensis.* London.

Blytt, A. (**1906**). *Haandbog i Norges Flora.* Oslo.

Braun-Blanquet, J. & Rübel, E. (**1933**). *Flora von Graubünden.* **2**. *Veröff. geobot. Inst. Rübel,* Hft. **7**. Bern and Berlin.

Brenchley, W. E. (**1911, 1912, 1913**). The weeds of arable land in relation to the soils on which they grow. I–III. *Ann. Bot., Lond.,* **25**, 155–65; **26**, 95–109; **27**, 141–66.

Brenchley, W. E. (**1920**). *Weeds of Farm Land.* London.

Britton, C. E. (**1929**). *Rep. B.E.C.* pp. 237–8.

Britton, C. E. (**1930**). *Rep. B.E.C.* pp. 522–3.

Britton, C. E. (**1933**). British Polygona, Section Persicaria. *J. Bot., Lond.,* **71**, 90–8.

Britton, C. E. (**1935**). *Rep. B.E.C.* p. 39.

Britton, C. E. (**1936**). *Rep. B.E.C.* p. 276.

Buchli, M. (**1936**). *Oekologie der Ackerunkräuter der Nordostschweiz. Beit. z. geobot. Landesaufnahme der Schweiz,* **19**. Bern.

Chiovenda, E. (**1920**). Nuova località italiana per il *Myriostoma coliliforme* (Dichs.) Corda. *Nuova Giorn. Bot. Ital.* Nuova Ser. **27**, 7–11. (Seen only in abstract: *Bot. Abstr.* **7**, 53, 1921.)

Clifford, M. H. (**1936**). A Mesolithic flora in the Isle of Wight. *Proc. Isle of Wight Nat. Hist. Arch. Soc.* **2**, 582–94.

Dorph-Petersen, K. (**1924**). Examinations of the occurrence and vitality of various weed seed species made at the Danish Seed-Testing Station during the years 1896–1923. *Rep. 4th Int. Seed-Testing Conf. London,* 1924, pp. 124–38.

Drabble, E. & H. (**1916**). Notes on the Flora of Derbyshire. *J. Bot., Lond.,* **54**, 133–39.

Druce, G. C. (**1892**). *Rep. B.E.C.* p. 384.

Druce, G. C. (**1897**). *The Flora of Berkshire.* Oxford.

Druce, G. C. (**1930**). *Rep. B.E.C.* p. 368.

Duvel, J. W. T. (**1905**). Vitality of buried seeds. *Bull. U.S. Dept. Agric. Pl. Ind.* **83**, 22.

Evershed, A. F. C. H. (**1918**). Pheasants and agriculture. *J. Agric. Sci.* **9**, 63–91.

Ewart, A. J. (**1908**). On the longevity of seeds. *Proc. Roy. Soc. Vict.* **21**, 1–210.

Ewart, A. J. (**1930**). *Flora of Victoria.* Melbourne.

Gentner, G. (**1929**). Beiträge zu einer Monographie der Provenienzen der Klee- und Grassaaten. *Actes du 5ème Cong. Int. d'Essais de Semences,* Rome, 1929, pp. 103–25.

Goss, W. L. (**1924**). The viability of buried seed. *J. Agric. Res.* **29**, 349–62.

Hermann, F. (**1912**). *Flora von Deutschland und Fennoskandinavien sowie von Island und Spitzbergen.* Leipzig.

Hill, A. W. (**1917**). The flora of the Somme battlefield. *Kew Bull. Misc. Inf.* **9** and **10**, 297–300.

Hooker, J. D. (**1890**). *The Flora of British India,* **5**. London.

Jaretsky, R. (**1927**). Einige Chromosomenzahlen aus der Familie der Polygonaceae. *Ber. dtsch. Bot. Ges.* **65**, 48–54.

Jaretsky, R. (**1928**). Histologische und karyologische Studien an Polygonaceen. *Jb. wiss. Bot.* **69**, 357–490.

Justice, O. L. (**1941**)' A study of dormancy in seeds of *Polygonum. Mem. Cornell Agric. Exp. Sta.* **235**, 43.

Komarov, V. L. (**1936**). *Flora U.S.S.R.* **5**. Leningrad.

Korsmo, E. (**1934**). *Explanation to Prof. Dr E. Korsmo's Weed Plates,* Series 1. Oslo.

Lindmann, C. A. M. (**1926**). *Svensk Fanerogamflora,* 2nd ed. Stockholm.

Long, H. C. (**1910**). *Common Weeds of the Farm and Garden.* London.

Long, H. C. (**1938**). *Weeds of Arable Land.* Bull. Minist. Agr. **108**. 2nd ed. London.

Moss, C. E. (**1914**). *Cambridge British Flora,* **2**. Cambridge.

Pammel, L. H. (**1910**). *Weeds of the Farm and Garden.* New York.

Praeger, R. L. (**1913**). On the buoyancy of the seeds of some Britannic plants. *Sci. Proc. Roy. Dubl. Soc.* **14**, 13–62.

Reid, C. (**1899**). *The Origin of the British Flora.* London.

Salisbury, E. J. (**1921**). Vegetation of drying mud and retarded germination. *Naturalist,* 1920–1, pp. 329–32, 365–6.

Salisbury, E. J. (**1932**). The East Anglian flora. *Trans. Norf. Norw. Nat. Soc.* **13**, 191–263.

Salter, J. H. (**1935**). *The Flowering Plants and Ferns of Cardiganshire.* Cardiff.

Scott-Elliot, G. F. (**1896**). *The Flora of Dumfriesshire.* Dumfries.

Small, J. K. (**1913**). *Flora of the South-Eastern United States,* 2nd ed. New York.

Smith, K. M. (**1937**). *A Textbook of Plant Virus Diseases.* London.

Stapledon, R. G. (**1942**). In address to the Summer Meeting of the British Ecological Society, London, 1942 (unpublished.)

Thomson, G. M. (**1922**). *The Naturalisation of Animals and Plants in New Zealand.* Cambridge.

Volkart, A. (**1924**). Report on the provenance of grass and clover seed. *Rep. 4th Int. Seed-Testing Conf.* pp. 83–97. London.

Woodcock, E. F. (**1914**). Observations on the development and germination of the seed in certain Polygonaceae. *Amer. J. Bot.* **1**, 454–76.

Polygonum lapathifolium L. (*P. tomentosum* Schr. of many continental authors)

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Sect. PERSICARIA. Stem usually erect, branched or not, or, when decumbent, rarely branched from the base; to 1 m. in height, usually much less. Pigmentation very variable. Leaves, especially the lower, more or less hairy, variable in size and shape, often glandular, blotched or not. Ocreae tight, not or only shortly ciliate. Inflorescences 1 to many, the peduncles usually densely glandular. Racemes dense, variable in size and shape,
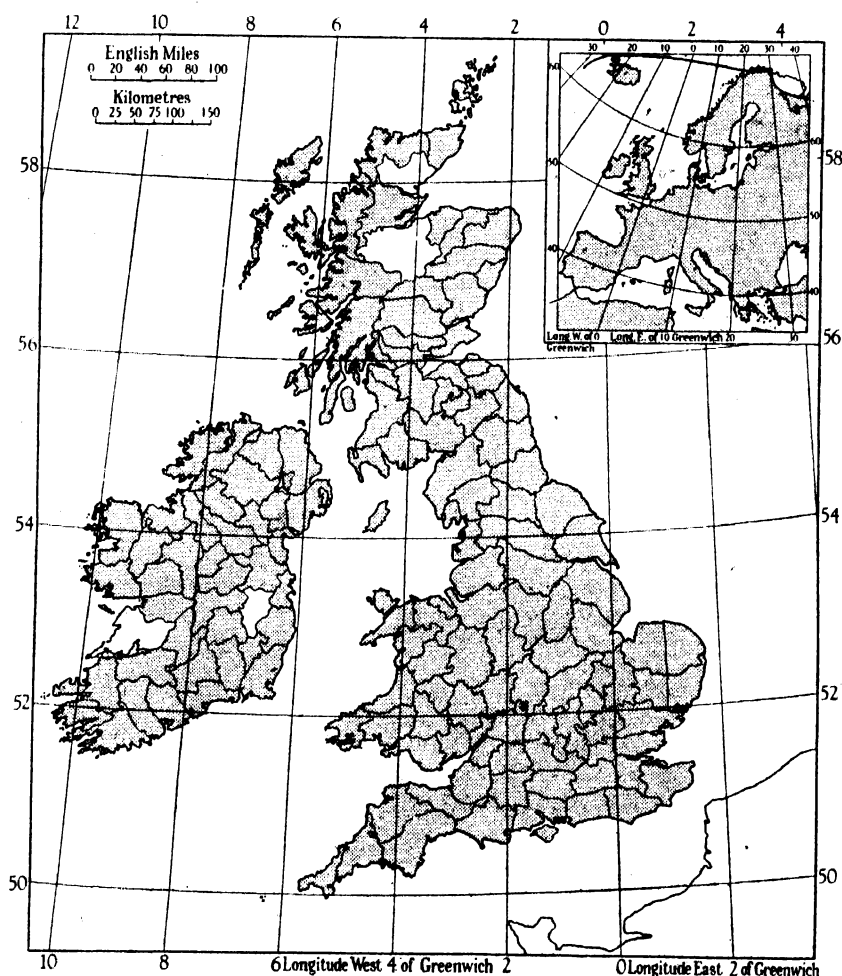
Fig. 1. *Polygonum lapathifolium* L.: vice-comital distribution in the British Isles, and (inset) distribution in Europe.

usually erect. Perianth greenish-white, less commonly red or pink, glandular, the main veins raised and with recurved branches. Styles 2, united at the base only. Fruits about $2 \cdot 5 \times 2 \cdot 5$ mm., black, shining, orbicular, biconcave, a few trigonous ones sometimes present, equal to or longer than the perianth.

Distinguished from *P. persicaria* by the leaf tomentum and characters of the fruit

and fruiting perianth and from *P. petecticale* by the fruit and perianth only. (See *P. persi-caria*, Fig. 1). Other differences are inconstant.

Some continental writers refer to *P. lapathifolium* L. as a synonym of *P. nodosum* Pers., a species now called *P. petecticale* in Britain. *P. tomentosum* Schr. has sometimes been regarded as synonymous with *P. petecticale* (Stokes) Druce, but the descriptions in Aschers. & Graebn. **4**, p. 809, Blytt (1906, p. 288), Lindmann (1926, p. 238), Danser (1921), etc. leave no doubt that their *P. tomentosum* Schr. refers to the plant here called *P. lapathi-folium* L. and that their *P. nodosum* Pers. is the same as our *P. petecticale* (Stokes) Druce. Dyer & Trimen (1871), however, state that *P. nodosum* Pers. is the same as *P. persicaria* var. *elatum* Gren. & Godr. The best general account of taxonomy and synonymy is that of Danser (1921, pp. 140–67), who also deals with *P. petecticale*.

A very variable species of which many varieties have been described (see e.g. Britton, 1933). By sowing experiments, Danser (1921), working on this species and *P. petecticale*,
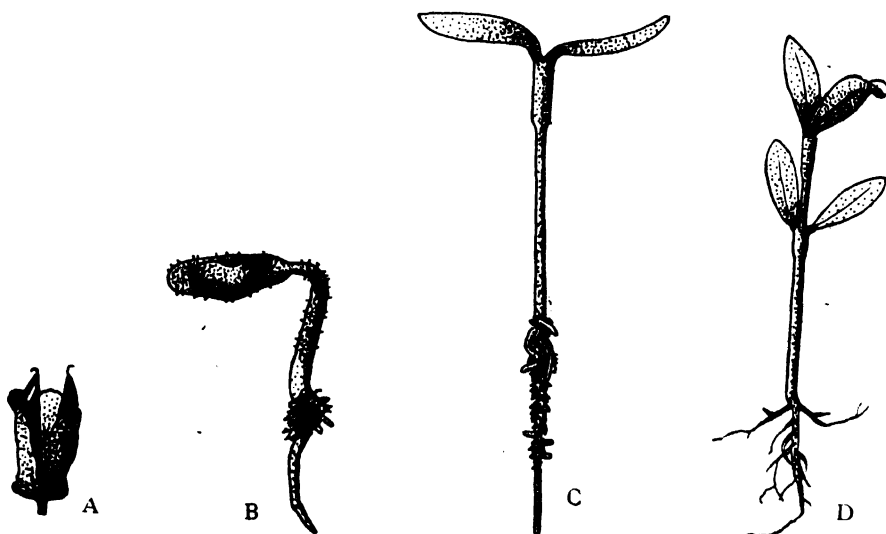
Fig. 2. Seedlings of *P. lapathifolium* L. A, side view of nut split at the apex showing the adherent perianth, × 15. B, × 6. C, × 4·5. D, × 3.

showed that: (1) any one progeny was very constant within itself and true-breeding, (2) practically no two progenies were alike, (3) there was extreme plasticity in respect of height, branching, habit, leaf-size, tomentum, etc. (see V (*b*)), but that anthocyanin pigmentation of flowers, stems, nodes, leaves, etc. and leaf form were rather constant. On the basis of these constant characters he erected a complex system of classification including numerous subspecies, varieties and hybrids which, for reasons too numerous to detail here, cannot be accepted. His results, however, are important and valid and show that there exists great genetical diversity combined with plasticity. He correlated the constancy of a progeny with a high degree of autogamy (cf. VIII (*a*) and (*c*) below).

A native of Europe widely distributed as a weed of cultivation. Common in Britain but less so than *P. persicaria*, which it somewhat resembles ecologically.

I. *Geographical and altitudinal distribution.* Recorded for all English vice-counties except Linlithgow (84), Easterness (96), Mid-Ebudes (103) and East Sutherland (107) and all Irish except Clare (9) and Kildare (19) (Praeger, 1934, p. 524, who, however, gives a record for vice-county 19 in an earlier work (Praeger, 1909, p. 181)).

Perhaps less common in the north of Britain than in the south; all four 'English' vice-counties for which there is no record are Scottish.

Throughout Europe to *c.* 65° N. in Iceland (Moss, 1914, p. 117), *c.* 68° N. in Lapland (Lindmann, 1926, p. 238) and (probably) to 70° N. in Norway (Blytt, 1906, p. 288). Eastwards to Siberia (to 70° 20′ N. (Komarov, 1936, p. 649) and Far East, northern India, Malaysia, China, Japan, Australia, New Zealand. Also Asia Minor, Syria, Palestine, North Africa, from Egypt to Morocco, South Africa; North, Central, South America and the West Indies (Small, 1913, p. 378). Some of the records given above may apply to *P. petecticale*, which is generally 'lumped' with *P. lapathifolium*, but the account given is probably substantially correct.

Bentham (1870, p. 270) records the species in Queensland, Victoria, New South Wales and Tasmania, while the first record for New Zealand is 1899 (Thomson, 1922, p. 465). Has evidently increased and spread since that date in both Australia and New Zealand. A naturalized alien also in America and probably elsewhere, but no details are available.

Ascends to 7000 ft. (2130 m.) in the Himalaya (Hooker, 1890, p. 35), to 5940 ft. (1810 m.) in Central Europe (Moss, 1914, p. 117), to 3940 ft. (1200 m.) in the Tirol (Aschers. & Graebn. **4**, p. 811) and to 5910 ft. (1800 m.) in Graubünden (Braun-Blanquet & Rübel, 1933, p. 450). In Britain to 1200 ft. (365 m.) near Buxton (Alt. Range Br. Pl.) and 1000 ft. (305 m.) in Westmorland (Wilson, 1938, p. 210).

II. *Habitat.* Always in disturbed communities: a weed of arable land, ditches, manure heaps, etc. Similar to *P. persicaria* but generally less common and less widely tolerant than that species.

As an arable weed it has been seen on sand (*p*H 6·6–6·9 (colorimetric)) at Dersingham, Norfolk, and in east Dorset (acid); on heavy clay in Bedfordshire and north Suffolk; on black fen peat in Cambridgeshire (*p*H 6·9–7·2 (colorimetric)), where it is generally more common than *P. persicaria*. Occurs on river mud (probably basic) at Barton Mills, Suffolk, and is recorded by Hegi (*Fl.* **3**, p. 199) as sometimes floating; on the mud banks of Wicken Lode, Cambridgeshire (1943, 1944) and is said by Druce (1926, p. 286) to occur on mud newly dredged from rivers and ponds in Bucks. (cf. *P. petecticale* and see VIII below). Recorded by Robinson (1902, p. 169) on the Hull dock wastes, by Scott-Elliot (1896, p. 150) on railway cinders and has been seen on sand and manure heaps.

On the sea-coast of Norway (Blytt, 1906, p. 288) and in the fens and salt-marshes of north Germany (Hegi, *Fl.* **3**, p. 200). There appears to be no British record of it as a maritime plant.

Evidently extremely tolerant of a wide range of edaphic conditions and appears to require chiefly disturbance and reduction of competition.

P. Greig-Smith has found plants of this species on Swaffham Prior Fen, Cambridgeshire, affected with a chlorotic mottling. Sugar beet in the same field showed symptoms of manganese deficiency and it is possible that this also was the cause of the mottling in our species.

III. *Communities.* There is no information about association with crops, but it has been seen in potatoes, wheat, beans, cabbages, sprouts and sugar-beet. In beet at Waterbeach, Cambridgeshire, it was associated with *Polygonum convolvulus, P. aviculare, Chenopodium album* and 'volunteers' from a previous cereal crop. See also List 3 for *P. persicaria.* In Brussels sprouts at Lower Mannington, Dorset, its associates were *Rumex acetosella, Plantago lanceolata, Arrhenatherum elatius, Spergula sativa* (?), *Filago*

minima, *Achillea millefolium*, *Poa annua*, *Holcus mollis*, *Polygonum persicaria*. In an uncultivated part of the same field there was a dense stand of the species associated with *Achillea millefolium*, o., *Anthemis cotula*, r., *Capsella bursa-pastoris*, a., *Leontodon autumnalis*, o., *Plantago lanceolata*, o., *Polygonum persicaria*, o., *Sonchus asper*, r., *Tussilago farfara*, l., *Zea mays* (volunteer), r.

Abundant on the newly-made mud banks of Wicken Lode, Cambridgeshire, in 1943; in 1944 the vegetation had become much more dense and *P. lapathifolium* had become, locally at least, much less common. A list made in 1944 includes: *P. lapathifolium*, *Alopecurus agrestis*, *Chenopodium* sp., *Potentilla anserina*, *Capsella bursa-pastoris*, *Poa pratensis*, *Polygonum aviculare*.

A semi-closed community on a ditch-bank at Horton Heath, Dorset, was composed of *Polygonum hydropiper*, *P. persicaria*, *P. lapathifolium*, *P. aviculare*, *Ranunculus repens*, *Dactylis glomerata*, *Rumex conglomeratus*, *Potentilla anserina*, *Filipendula ulmaria*, *Poa trivialis*, *Cerastium semidecandrum*, *Anthemis cotula*, *Galium palustre*. A very open community on uncultivated ground at the Plant Breeding Institute, Cambridge, was made up of *Senecio vulgaris*, *Chenopodium album*, *Capsella bursa-pastoris*, *Polygonum aviculare*, *P. lapathifolium*, *Poa annua*, *Sonchus oleraceus*, *Anagallis arvensis*, *Veronica persica*, *Trifolium repens*.

In general, characteristic of open communities and associated with other weeds. Appears to be even less tolerant of competition than *P. persicaria*; see, e.g., lists (1), (2) and (4) for that species which represent more or less closed communities. The community listed under (5) was very much more open. Regarded as a less serious weed than *P. persicaria*; unrecorded by Brenchley (1920), while in the 'Dreifeldwirtschaftgebiet' of Switzerland Buchli (1936, p. 60) states that it has a frequency of 3·7 % of all fields studied as against 19·5 % for *P. persicaria*.

IV. *Response to biotic factors*. In one case where the top of the plant had been removed, there was increased production of short flowering branches from the lower leaf axils.

V. (a) *Gregariousness*. Solitary, a few plants together, or in dense stands.

(b) *Performance in various habitats*. Crowding appears to affect habit in the same way as in *P. persicaria* (q.v.).

For comment on plasticity in relation to taxonomy, see introduction. Danser (1921) working on this species and *P. petecticale* states that the expression of heritable characters is much affected by the environment; thus in 'dry, sterile' situations all the varieties resemble each other, the leaves are small and tomentose, the inflorescences are small and little-branched and the fruits are small. In fertile situations, on the other hand, the plant is larger and more branched, the stems are thick, the leaves large and there is less colour, the last-named also being less in the shade than in the sun (this is common in other species). With regard to habit he states that all varieties are known to have erect forms but that not all have prostrate ones, and suggests that the conditions necessary for the production of the prostrate habit are different for different varieties. He also notes that swollen nodes are characteristic of damp, rich situations and that the leaf-tomentum is always more on the lower than on the upper leaves and is much affected by humidity.

(c) *Effect of frost, drought, etc.* Danser (1921) suggests that drought may cause poor fruit development and sterility, as in the dry summer of 1911 in Holland.

VI. (a), (b) *Morphology, etc.* Main root from 3 to about 20 cm. in length. Adventitious roots may arise from the lower nodes where these are buried or touching the soil surface.

(c) *Mycorrhiza.* Not recorded.

(d) *Perennation.* Summer annual (therophyte).

(e) *Vegetative reproduction.* Not known to occur.

(f) *Longevity.* One season only, roughly from spring to autumn.

(g) *Age at first flowering.* About 6 weeks after germination in pots outdoors. As little as 4 weeks in one case in a greenhouse (P. W. Richards).

(h) *Frequency of seed production.* Every year, so far as is known.

(i) *Ecotypes.* No information.

(j) *Chromosome number.* A diploid with somatic number 22 (Jaretsky, 1928, p. 417). Confirmed on root-tips of British material by the writer.

Ten pollen grains had a mean diameter of 40·3 μ (s.e.m. 0·72) and an approximate mean volume of 34,200 μ^3. The diameter measurements differ significantly from those of *P. persicaria* (q.v.) and are consonant with the fact that the latter species is a tetraploid.

Pollen production is very low (i.e. about 30 pollen grains per anther) and the very low ratio of pollen grains to ovules (say about 200) is suggestive of inbreeding (cf. notes on the constancy of progenies in the introduction to this account and VIII (*a*)). In addition, in one plant examined, about 50 % of the pollen grains had germinated in the anthers and, though it could not be shown that these were effective in fertilization, such behaviour is reminiscent of the cleistogamic flowers of *Viola odorata* var. *praecox* (Madge, 1929).

VII. *Phenology.* (a) Time of maximum root growth not known.

(b) Non-flowering shoots have not been seen. Short axillary or basal flowering branches may be produced from about July onwards.

(c) Flowers from June or July to September.

(d) Mature fruits seen in Dorset in mid-July 1943, but this is perhaps earlier than usual.

(e) A spring germinator. See VIII (*j*), below.

VIII. (a) *Mode of pollination.* As for *P. persicaria* (Knuth, *Poll.* 3, p. 347).

(b) *Insect visitors.* Dr Morison has found *Taeniothrips atratus* (Hal.) and *T. vulgatissimus* (Hal.) on this species.

(c) *Apomixis.* Not recorded.

(d) *Cleistogamy.* Not recorded but the premature pollen-tube growth noted in VI (*j*) is suggestive.

(e) *Vivipary.* Not recorded.

(f) *Hybrids.* A number of hybrids have been claimed on taxonomic grounds. Britton (1930, 1936) records × *P. persicaria* and Aschers. & Graebn. 4, p. 812, give × *P. persicaria* × *P. petecticale*, and × *P. hydropiper*. Britton (1930) states that the cross × *P. persicaria* bore well-formed fruits, but that they were empty. Danser (1921), however, states that he found no sterile hybrids and that sterility, when it did occur, was due rather to adverse environmental conditions such as drought. He calls the × *P. petecticale, P. mesomorphum* Danser and states that it occurs with its presumed parents, other intermediate forms being much less common even than the hybrid itself. He also states that it is fertile and true-breeding, which seems unlikely (in the absence of apomixis, etc.).

For comment on the bearing of cytology on these hybrids, see *P. persicaria.*

(g) *Amount of seed.* 1 seed per fruit; from 10 to about 1500 fruits per plant. Korsmo (1934, p. 11) gives 800–850 nuts per plant.

Fruit weight: four samples of 25 fruits weighed respectively 104·4, 109·9, 117·0 and

118·6 mg., giving a mean of 4·5 mg. per fruit. Korsmo (*loc. cit.*) gives 3·6 mg. and Pammel (1910, p. 28) gives 1·56 mg. Evidently very variable.

(*h*) *Dispersal.* Mature fruits fall or are knocked off the parent plant. Distribution possibly by animals (cf. *P. persicaria*), but the only available records are those of Ridley (*Disp. Plts.* pp. 484, 492), who states that the fruits were eaten by *Colaptes auratus* L. (the flicker) in America and by *Anas strepera* L. (the gadwall) which is widely migratory over the temperate zone. (No record of viability.) Praeger (1913) states that the fruits float for one day, but there is no evidence of water dispersal.

The fruits are given by Long (1910, pp. 369, 370) as an impurity of grass and clover seed but there is no record of their occurrence in the samples tested at the Official Seed Testing Station, Cambridge, in the season 1942–3. The fruits may not, however, have been distinguished from those of *P. persicaria* (q.v.). Volkart (1924) and Gentner (1929) have reported on the impurities of red clover samples from many different European localities. From their data it appears that there are about 25 nuts of *P. lapathifolium* to 1000 seeds of clover, on the average. Knowing the seed weight and seed-rate for red clover, it can be calculated that roughly 78,000 fruits will be sown per acre in pure red clover and 25,000 in mixtures. These figures are equivalent to about 19 and 6 fruits per sq.m. respectively. These calculations are only very approximate but serve to illustrate the importance of agricultural seeds and seed mixtures as a means of spread, particularly when it is remembered that there is a considerable international trade in seed.

(*i*) *Viability.* See (*j*).

(*j*) *Conditions for germination.* Justice (1941) and Ransom (1935) showed that a period of after-ripening is necessary which is markedly shortened by subjecting the saturated fruits to low temperatures for a period of months. The dry fruits do, however, ripen slowly at ordinary temperatures though the figures available show wide variation: thus, in four tests, the writer has obtained 58, 0 and 0 % germination in soil after 10 months' storage and 12 % (in both light and dark) in the laboratory. Germination was more or less 'simultaneous'. Dorph-Petersen (1924) gives the following germination figures for 1–8 years' dry storage: 86, 96, 79, 48, 23, 7, 0, 0 % respectively.

Justice (*loc. cit.*) showed that constant temperatures slightly above freezing (as against alternating temperatures) were most favourable to after-ripening, nuts thus after-ripening relapsing into secondary dormancy if dried. He also showed that outdoor burial in soil in winter was effective, while Dorph-Petersen (*loc. cit.*) notes that 99 % of nuts placed in soil shortly after harvest germinated, mostly in the following spring.

The above data apply to intact nuts: the pericarp was shown by Justice to retard the process of after-ripening. He found that intact nuts 4 months after harvest did not germinate, while nuts from which the pericarp had been removed gave 22 %. He suggested (as did Ransom, 1935) that the pericarp inhibited gaseous exchange and thus retarded after-ripening. This is consistent with the (probable) retention of viability of nuts in mud in ponds, etc. (cf. II), where oxygen supply is limited.

It appears, therefore, that low winter soil temperatures and saturation are the factors conditioning the spring-germinating habit of this species, while gaseous exchange may be limiting for after-ripening in the case of nuts deeply buried in soil or mud (cf. the effects of deep ploughing). It may be also that the generally higher temperatures at depth in soil in winter are partly responsible. There are records of viable nuts being

present in soil (e.g. Buchli, 1936, p. 221, in Switzerland), but no details are available about period of viability.

Buchli (1936, p. 238) placed samples of 500 fruits in bags and buried them in dung, withdrawing and testing samples after a fortnight, one month and two months. Samples buried at the surface gave respectively 17, 14 and 5 % germination while those buried at a depth of 0·5 m. gave 14, 1 and 1 %. Depth and period of burial thus both appear to affect viability.

(k) *Morphology of seedlings.* Nut splits at the apex and radicle appears. Hypocotyl elongates and carries up the remains of the nut attached to the cotyledons, which are red when first exposed and remain red in the dark; they bear numerous small glands visible at a very early stage but particularly clearly seen at the margins of the older cotyledons, which are oblong, fleshy, dark green flushed with red above and red below. The ocrea can easily be distinguished at the base of the first foliage leaves, which are generally tomentose. The seedlings can thus be distinguished from those of *P. persicaria* by the glands and tomentum, but not from those of *P. petecticale*.

(l) *Effective reproduction.* Entirely by seed.

IX. *Pests, parasites.* See *Polygonum* L. Virus: given by Smith (1937, p. 25) as a weed host of Beta Virus 1 (curly-top), in America.

X. *History.* Reid (1899, p. 139) gives a (doubtful) Neolithic record for Cowden Glen, Renfrewshire. At Glastonbury, the fruits have been found with remains of other weeds and cereals in an Iron-Age deposit (Conolly).

Classified by Buchli (1936, p. 90) as an 'archaeophyte', i.e. a species having no known 'natural' habitat, always associated with human disturbance (cf. *P. persicaria*).

REFERENCES

Bentham, G. (1870). *Flora Australiensis.* London.

Blytt, A. (1906). *Haandbog i Norges Flora.* Oslo.

Braun-Blanquet, J. & Rübel, E. (1933). *Flora von Graubünden,* 2. *Veröff. geobot. Inst. Rübel,* Hft. 7. Bern and Berlin.

Brenchley, W. E. (1920). *Weeds of Farm Land.* London.

Britton, C. E. (1930). *Rep. B.E.C.* p. 522.

Britton, C. E. (1933). British Polygona, Section Persicaria. *J. Bot., Lond.,* 71, 90–8.

Britton, C. E. (1936). *Rep. B.E.C.* p. 276.

Buchli, M. (1936). *Oekologie der Ackerunkräuter der Nordostschweiz. Beit. z. geobot. Landesaufnahme der Schweiz,* 19. Bern.

Danser, B. H. (1921). Contribution à la systématique du *Polygonum lapathifolium. Rec. trav. bot. néerl.* 18, 125–210.

Dorph-Petersen, K. (1924). Examinations of the occurrence and vitality of various weed seed species made at the Danish Seed-Testing Station during the years 1896–1923. *Rep. 4th Int. Seed-Testing Conf. London,* pp. 124–38.

Druce, G. C. (1926). *The Flora of Buckinghamshire.* Arbroath.

Dyer, W. T. T. & Trimen, H. (1871). On *Polygonum nodosum. J. Bot., Lond.,* 9, 33–8.

Gentner, G. (1929). Beiträge zu einer Monographie der Provenienzen der Klee- und Grassaaten. *Actes du 5ème Cong. Int. d'Essais de Semences, Rome,* pp. 103–25.

Hooker, J. D. (1890). *The Flora of British India.* London.

Jaretsky, R. (1928). Histologische und karyologische Studien an Polygonaceen. *Jb. wiss. Bot.* 69, 357–490.

Justice, O. L. (1941). A study of dormancy in seeds of *Polygonum. Mem. Cornell Agric. Exp. Sta.* 235, 43.

Komarov, V. L. (1936). *Flora U.S.S.R.* 5. Leningrad.

Korsmo, E. (1934). *Explanation to Prof. Dr E. Korsmo's Weed Plates,* Series 1. Oslo.

Lindmann, C. A. M. (1926). *Svensk Fanerogamflora,* 2nd ed. Stockholm.

Long, H. C. (1910). *Common Weeds of the Farm and Garden.* New York.

Madge, M. A. P. (1929). Spermatogenesis and fertilisation in the cleistogamous flowers of *Viola odorata* var. *praecox* Gregory. *Ann. Bot., Lond.*, **43**, 545–79.

Moss, C. E. (1914). *Cambridge British Flora,* **2.** Cambridge.

Pammel, L. H. (1910). *Weeds of the Farm and Garden.* New York.

Praeger, R. L. (1909). *A Tourist's Flora of the West of Ireland.* Dublin.

Praeger, R. L. (1913). On the buoyancy of the seeds of some Britannic plants. *Sci. Proc. Roy. Dubl. Soc.* **14**, 13–62.

Praeger, R. L. (1934). *The Botanist in Ireland.* Dublin.

Ransom, E. R. (1935). The inter-relations of catalase, respiration, after-ripening and germination in some dormant seeds of the Polygonaceae. *Amer. J. Bot.* **22**, 815–25.

Reid, C. (1899). *The Origin of the British Flora.* London.

Robinson, J. F. (1902). *The Flora of the East Riding of Yorkshire.* London.

Scott-Elliot, G. F. (1896). *The Flora of Dumfriesshire.* Dumfries.

Small, J. K. (1913). *Flora of the South-Eastern United States,* 2nd ed. New York.

Smith, K. M. (1937). *A Textbook of Plant Virus Diseases.* London.

Thomson, G. M. (1922). *The Naturalisation of Animals and Plants in New Zealand.* Cambridge.

Volkart, A. (1924). Report on the provenance of clover and grass seed. *Rep. 4th Int. Seed-Testing Conf. London,* pp. 83–97.

Wilson, A. (1938). *The Flora of Westmorland.* Arbroath.

Polygonum petecticale (Stokes) Druce (*P. maculatum* Trimen & Dyer,
P. nodosum Persoon, etc.)

N. W. SIMMONDS

Sect. PERSICARIA. Stem erect, decumbent or prostrate, to more than 1 m. in height, usually with dark spots and otherwise pigmented. Ocreae loose, shortly or not ciliate. Leaves more or less tomentose, variable in size, shape, colour, etc. Inflorescences 1 to many, the peduncles glandular or nearly glabrous, erect or drooping, usually slender. Perianth dirty pink, sometimes red or whitish, more or less glandular, longer than the
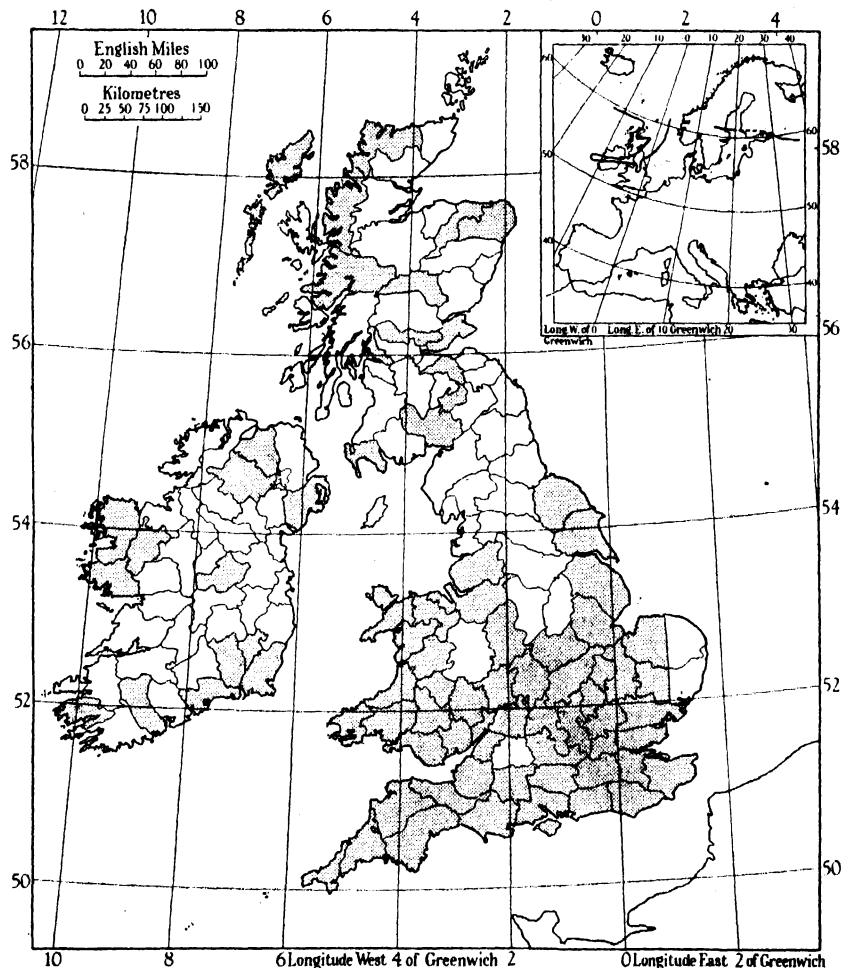
Fig. 1. *P. petecticale* (Stokes) Druce: vice-comital distribution in the British Isles and (inset) European distribution so far as it is known.

mature fruit, which is biconcave (a few trigonous ones are sometimes present), ovate, c. 2×1.5 mm., dark brown in colour. Plastic, extremely variable. Distinguished from *P. lapathifolium* (q.v.) by the fruit characters only (see *P. persicaria*, Fig. 1), but there is generally a difference in 'aspect' also. The anthers are commonly pink or red and this may prove to be of diagnostic value, especially in the absence of fruits, though it has,

as yet, been insufficiently tested. For a general account of taxonomy, variability and nomenclature, see *P. lapathifolium*.

A species of open or intermittent habitats, especially characteristic of drying mud; uncommon, or at least sporadic, in Britain.

I. *Geographical and altitudinal distribution.* Recorded for seventy English and thirteen Irish vice-counties, but these records are probably incomplete. Thus Praeger (*Ir. Top. Bot.* p. 272) says 'not distinguished in Ireland and range unknown'. Native in England, doubtfully so in Ireland. Praeger (*Bot. Irl.* p. 278) says of Rosslare: 'the only place in Ireland where it has the appearance of a native'. An uncommon plant in southern England and becomes even less common in the north, though this may be due in part to a deficiency of records. May be sporadically abundant on exposed mud (see II, below).

Generally distributed through Europe to about 61° N. in Sweden (Lindmann, 1926, p. 239). Russia, Siberia and Far East (Komarov, 1936, p. 650); Lebanon and Afghanistan (Dyer & Trimen, 1871); northern India (Hooker, 1890, p. 35); N. Africa (Moss, 1914, p. 118); Portuguese East Africa (Dyer, 1913, **6**, pt. 1, p. 108); S. Africa (Moss, 1914); Japan; Australia, Canada, the U.S.A. and South America (Argentine and Chile) (Irigoyen & Thellung, 1919).

Lowland; altitudinal range in Britain not recorded. In Graubünden, ascends to 1070 m. (3500 ft.) (Braun-Blanquet & Rübel, 1933, p. 450).

II. *Habitat.* In disturbed habitats such as arable land, ditches, etc. and peculiarly characteristic of exposed lake or river mud.

It has been seen on sand (*p*H 6·6–6·9 (colorimetric)) at Dersingham, Norfolk; on the mud banks of Wicken Lode, Cambridgeshire; on a silty river alluvium at Coe Fen and on dried mud dredged from a ditch at Sheep's Green, Cambridge. Recorded on mud dredged from rivers or ponds or in dried-up ponds, reservoirs, etc. by Amphlett & Rea (1909, p. 311), Druce (1897, p. 428, 1926, p. 287, 1930, p. 197), Horwood & Gainsborough (1933, p. 464), Purchas & Ley (1889, p. 254) and Salisbury (1921, pp. 365–6). It is probable that viable fruits are present in the mud in such cases and germinate only on exposure (see VIII (*h*), below). Said by Salisbury (1942, p. 200) to be one of the more characteristic species of drying mud.

III. *Communities.* In a bean crop at Dersingham, Norfolk, it was very rare and associated with *P. persicaria*, *P. lapathifolium*, *Cirsium lanceolatum* and *Chenopodium album*. Two lists from Coe Fen, Cambridge, were: ((1) (1943) *Alopecurus geniculatus*, *Apium nodiflorum*, *Catabrosa aquatica*, *Glyceria aquatica*, *Nasturtium officinale*, *Polygonum hydropiper* and *Ranunculus repens*; (2) (1944) *Ranunculus sceleratus*, *Agrostis* sp., *Glyceria fluitans*, *Polygonum hydropiper* and *P. persicaria*. Sporadic in its occurrence on Coe Fen in the years 1942–3–4; present in each year, but appeared in slightly different stations. All three communities were fairly open. On Sheep's Green, Cambridge (1944), on dried and cracked mud dredged from a drain the previous winter, it was occasional and associated in one spot with *Urtica dioica*, *Cirsium arvense* and *Capsella bursa-pastoris*. The vegetation here was frequently so open that the over-ground parts of one plant were not touching those of any other.

IV. *Response to biotic factors.* Grazing by cattle (Sheep's Green, Cambridge, 1944) appears to lead to the production of numerous short axillary shoots and a dense, prostrate, almost cushion-like habit. Flowering is also much reduced.

V. (*a*) *Gregariousness.* Solitary, a few plants together or in large amount.

(b) *Performance in various habitats.* Plastic (see *P. lapathifolium*). Small, hairy, depauperate plants are found as in *P. persicaria* (q.v., V (b)) and *P. lapathifolium*, which are probably forms, but the nature of the environmental conditions producing them is not known.

There are specimens in the Cambridge University Herbarium from Portsfield, near Chichester, critically examined by C. E. Salmon. One specimen was 'normal' from the edge of a dried-up pool, while another, from inside the depression, was small, prostrate and stunted. *Bidens tripartita* was said to behave in a similar manner, the suggestion being that the plant in the depression was a form only.

Salisbury (1921, p. 365) states that exposed leaves of the var. *salicifolium* (see Moss, 1914, p. 118) were only slightly tomentose while shaded leaves were densely so, the difference also occurring on single leaves part shaded and part exposed.

(c) *Effect of frost, drought, etc.* No information.

VI. (a), (b) *Morphology.* Similar to *P. lapathifolium*.

(c) *Mycorrhiza.* Not recorded.

(d) *Perennation.* Summer annual (therophyte).

(e) *Vegetative reproduction.* Not known to occur.

(f) *Longevity.* One season only, roughly from spring to autumn.

(g) *Age at first flowering.* A few months.

(h) *Frequency of seed production.* As often as the parent plants occur, so far as is known.

(i) *Ecotypes.* No information.

(j) *Chromosome number.* Somatic number 22; 11 in pollen-grain division (Jaretsky 1928, p. 417). Not verified on British material, but 16 pollen grains had a mean diameter of 38·1 μ (S.E.M. 0·835) and did not differ significantly from *P. lapathifolium* in this respect. Pollen production very low.

VII. *Phenology.* (a) Time of maximum root growth not known.

(b) Non-flowering shoots have not been seen; new flowering shoots are produced during the summer.

(c) Flowers from June or July to September.

(d) Fruits mature from July or August onwards.

(e) Time of germination spring or early summer.

VIII. (a) *Mode of pollination.* No information, but the flower is similar to that of *P. lapathifolium*.

(b) *Pollinating insects.* No information.

(c) *Cleistogamy.* Not recorded.

(d) *Apomixis.* Not recorded.

(e) *Vivipary.* Not recorded.

(f) *Hybrids.* Several hybrids have been claimed on taxonomic grounds. Britton (1933) and Moss (1914, p. 118) give × *P. hydropiper* and Aschers. & Graebn. (4, p. 814) record × *P. persicaria*, × *P. lapathifolium*, × *P. hydropiper*, × *P. minus* and × *P. mite*. There is in the Cambridge University Herbarium a specimen labelled × *P. persicaria* which, though presumably a triploid, bears abundant fruit, which is, indeed, necessary for its determination. See *P. lapathifolium* (VIII (f)) for comment on the hybrid, *P. mesomorphum* Dans. There is no record of ecological behaviour.

(g) *Amount of seed.* One seed per fruit; from ten to about 2500 fruits per plant. Salisbury (1942, p. 200) states that five small plants bore respectively 170, 455, 553, 587

and 1074 fruits, one medium-sized plant bore 9200, while he estimates a large plant to produce about 25,000, the average being greater than 2000 fruits per plant. Evidently very variable in this, as in all other respects.

Fruit weight: four samples of 25 fruits weighed respectively 22·2, 22·4, 24·1 and 24·3 mg. giving an average of 0·9 mg. per fruit.

(*h*) *Dispersal.* Said by Horwood & Gainsborough (1933, p. 464) to be dispersed by wildfowl. The fruits float for 3 days according to Praeger (1913) and this, together with the records on river mud, suggests that water dispersal may occur.

(*i*) *Viability.* (See (*j*).

(*j*) *Conditions for germination.* No direct information. Perhaps similar to *P. lapathifolium*, but differing in having a longer period of after-ripening associated

Fig. 2. *P. petecticale* (Stokes) Druce: an early stage in germination. Note the characteristic form of the nut and perianth. Later stages cannot be distinguished from *P. lapathifolium* L.

with stronger inhibition by the pericarp. All ordinary germination tests have failed, but H. W. Howard has obtained 60 % in a sample of 10 nuts, dried for 1 year, by chipping the pericarp, a parallel untreated sample giving 0 %. Viable in submerged mud for considerable periods (cf. II), though exact information is lacking. The biology of germination is probably of critical importance for the ecology of this species; clearly, much more information is needed.

(*k*) *Morphology of seedlings.* See Fig. 2 for an early stage in germination showing the characteristic fruit and perianth. Later stages cannot be distinguished from *P. lapathifolium* (q.v.).

(*l*) *Effective reproduction.* Entirely by seed.

IX. *Parasites, diseases.* See *Polygonum* L.

X. *History.* No information.

REFERENCES

Amphlett, J. & Rea, C. (1909). *The Botany of Worcestershire.* Birmingham.

Braun-Blanquet, J. & Rübel, E. (1933). *Flora von Graubünden. Veröff. geobot. Inst. Rübel,* Hft. **7.** Bern and Berlin.

Britton, C. E. (1933). British Polygona, Section Persicaria. *J. Bot., Lond.,* **71,** 90–8.

Druce, G. C. (1897). *The Flora of Berkshire.* Oxford.

Druce, G. C. (1926). *The Flora of Buckinghamshire.* Arbroath.

Druce, G. C. (1930). *The Flora of Northamptonshire.* Arbroath.

Dyer, W. T. T. & Trimen, H. (1871). On *Polygonum nodosum. J. Bot., Lond.,* **9,** 33–8.

Dyer, W. T. T. (1913). *Flora of Tropical Africa,* 6, pt 1. London.

Hooker, J. D. (1890). *The Flora of British India,* 5. London.

Horwood, A. R. & Gainsborough, Earl of (1933). *The Flora of Leicestershire and Rutland.* Oxford.

Irigoyen, L. H. & Thellung, A. (1929). Étude sur le *Polygonum lapathifolium* L. en Amérique du Nord, avec quelques considérations sur cette espèce en Argentine. *Vierteljahrschr. Naturforsch. Ges. Zürich,* **74,** 244–53.

Jaretsky, R. (1928). Histologische und karyologische Studien an Polygonaceen. *Jb. wiss. Bot.* **69,** 357–490.

Komarov, V. L. (1936). *Flora U.S.S.R.* **5.** Leningrad.

Lindmann, C. A. M. (1926). *Svensk Fanerogamflora,* 2nd ed. Stockholm.

Moss, C. E. (1914). *Cambridge British Flora,* 2. Cambridge.

Praeger, R. L. (1913). On the buoyancy of the seeds of some Britannic plants. *Sci. Proc. Roy. Dubl. Soc.* **14,** 13–62.

Purchas, W. H. & Ley, A. (1889). *A Flora of Herefordshire.* Hereford.

Salisbury, E. J. (1921). Vegetation of drying mud and retarded germination. *Naturalist,* 1920–1, pp. 329–32, 365–6.

Salisbury, E. J. (1942). *The Reproductive Capacity of Plants.* London.

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THE VEGETATION OF SOME HILLSIDES IN UGANDA

ILLUSTRATIONS OF HUMAN INFLUENCE IN TROPICAL ECOLOGY. II

BY A. S. THOMAS, *Department of Agriculture, Uganda*

GENERAL ASPECTS OF VEGETATION IN UGANDA

The six hillsides described in the first part of this paper (Thomas, 1945, Fig. 1) give a fair indication of the general aspect of the vegetation in this part of Uganda. On the Sese Islands, the pattern of a broad belt of forest and farms on the hilltops, of short, light, grassland on the hillsides and of a narrow strip of forest near the lake, is repeated on island after island. On the coast between Kampala and Jinja, and to a distance of 10 km. inland, the general pattern is of short grass on the hilltops and farms and forests in the valleys, as at Nansagazi.

Short grassland, thickets of elephant grass, and papyrus swamps—as at Mpambire—are typical of the country in the south-west of the area mapped. Around Kampala there is the complex of farms and elephant grass on the hills, and strips of shorter grassland in the valleys, such as that described at Kawanda.

To the north of Kawanda, the population becomes less dense and more of the land is under a cover of elephant grass; because of the more intense dry spells, the relict woody vegetation becomes that of open woodland and not of closed forest: woodland, such as that described at Kakinze, covers most of the hills to the north and east of this place; and the broad valleys are filled with coarse, tufted grassland broken by groups of trees and shrubs on and around the termite mounds which are scattered along them. Finally, the north-west of the district is largely composed of broad valleys covered with open grassland and low hills with belts of woodland, such as that described at Seyajongo.

There are three areas where the general aspect is different from any described, or from intergrades between the communities. First, to the north-west of Jinja, close to the Nile, there is the Mabira Forest, about 300 sq. km. in extent; this is made up of closed evergreen forest with patches of woodland and grassland on the rocky hilltops. Native tradition asserts that this forest is secondary and that the land formerly was covered with farms; this hypothesis is supported by the general appearance of the forest—the scarcity of large trees, the preponderance of quick-growing, soft-wooded species, and the abundance of climbing plants—and there seems no reason to doubt that the land used to be inhabited and that the people were killed or driven away by intertribal wars—for this area lay on the boundary of Buganda. It is probable also that the abundance of *Simulium damnosum*, a most obnoxious small biting fly which breeds in the River Nile, also drove people away, or at any rate discouraged them from returning to this area; and that the forest has spread and is still spreading over land which once was cultivated.

Secondly, the country north of the Mabira Forest, lying between the rivers Sezibwa and Nile, has a vegetation showing affinities with that of Busoga, the district east of the Nile; there are grasslands and woodlands, but they are somewhat different from those at Kakinze and Seyajongo. And, thirdly, another distinct area of vegetation is that between Nakasongola and Lake Kyoga, where the average rainfall is about 750 mm. per

annum. In this area there are grasslands and thickets similar to those of Karamoja district, which lies away to the north-east; and, as in Karamoja, it appears that the grassland represents the natural vegetation and the thickets are a type induced by over-grazing (Thomas, 1944).

But, although it is possible to convey an impression of the vegetation of a large area of country by giving only a general description of the vegetation and by omitting some of the less conspicuous zones in the catenas, yet it must be remembered that these smaller zones may play a very important part in the life of the community of men and of animals living on the hillsides. For example, in a description of the catena on Sese, it is a mistake to pay attention to the land vegetation only, for the fish are derived from the water of the lake; and fish play a most important role in the Sese economy, being the chief source of protein in the diet of the people and of their cash income.

Similarly at Mpambire the narrow strip of forest above the swamp is of great value to the people, as it is the source of their timber and firewood. The valley grassland at Kawanda is not very extensive nor is it a good type of pasture; but it is the only part available for the local herds to graze. Even the exposed rocks on the top of Kakinze hill are useful to the local people, as their surface is an excellent place on which to winnow grain or to dry foodstuffs.

It is on account of the significance of relatively small and inconspicuous features of topography and vegetation that it has seemed worth while to use the catena method and to give the descriptions in some detail. The African, who lives in a certain countryside, will regard it in quite a different light to that of a European observer; he regards the plants from the point of view of their utility as a source of food for men or animals, of fuel, of fibre or of medicines; he regards the soil mostly from the aspect of suitability for his crops; and he regards the weather from the aspects of crop production and of bodily comfort. And, of course, the question of water supply is of prime importance to man and to animals. It is these matters which determine the density of settlement and therefore have a great influence on the vegetation.

THE SECONDARY CHARACTER OF VEGETATION IN UGANDA

The present population around Kampala is dense—about 28 people per square kilometre is the average for the Mengo district, in which this strip of country is situated. There is a great concentration of people around Kampala and in the county of Kyadondo, which lies immediately to the north-east of the town. In the drier country to the north of the area, water supplies are scarce in the dry seasons and the population is much more sparse. But it seems that, on all the land area included in the map, it would be impossible to find a single square kilometre where the vegetation has not been altered by human influence, either by the cutting down of trees, or by cultivation, or by burning, or by the grazing of stock.

There are stretches of climax evergreen forest in some of the other wetter areas of Uganda, at altitudes ranging from about 700 m. in Bwamba, on the west of Ruwenzori Mountain, to about 1500 m. in the Kibale Forest on the east of the mountain; in these forests *Cynometra Alexandrii* is the dominant tree. It would be expected that under 'natural' conditions the whole of the area within about 50 or 60 km. of the northern shores of Lake Victoria, where the temperature is equable and the rainfall is well distributed, would be under evergreen forest. And, as *Cynometra Alexandrii* is the dominant

tree in climax forests with similar rainfall, at altitudes both above and below that of this area, and as it grows well when planted, it might be expected to be dominant here also in climax forest. Yet the species has not been reported here in the wild state: nor do any of the forests in Buganda, even in the large area of Mabira, appear to be climaxes; they are composed mostly of quick-growing, soft-wooded species, such as are replaced by *Cynometra* when it forms a climax forest. As *Cynometra Alexandrii* has a heavy hard wood, so difficult to work that it is not used by Africans except for fuel, the lack of the species cannot be attributed to removal for timber; it is much more likely that none of the present forests in Buganda has reached its climax.

There are relict patches of closed forest in some of the rocky hills to the north of Kawanda, a fact which indicates that closed forest at one time covered most of the land surface in those places where the average annual rainfall was 1000 mm. or more. In places where the rainfall was less, and where the dry spells were more marked, it seems that the 'natural' vegetation was of woodland on the hills and of more or less open grassland in the valleys; while the general aspect of the vegetation in these drier parts, such as at Kakinze and Seyajongo, has been altered to a considerable degree by human influence, yet it has not been so completely transformed as that of the wetter parts which had been under closed forest.

THE INFLUENCE OF MAN ON VEGETATION IN UGANDA

The most spectacular transformation of vegetation which man achieves in Uganda is to be seen when forest is cut down or destroyed to make clearings for cultivation; an area of tall closed forest may be felled and little trace may remain in one or two years—only a few rotting tree trunks may be left among the bananas or other crops which are planted. It often happens that some trees are retained, to provide shade or shelter, or for their edible fruits—species such as *Canarium Schweinfurthii*, *Garcinia Buchanani* or *Pseudospondias microcarpa*. The climber, *Landolphia florida*, is also retained, on account of its large edible acid fruits.

Similar clearings are also made in the woodland communities of drier areas to the north; sometimes, as at Kakinze, many of the trees also are not cut down, but are merely coppiced and, after one or two crops have been harvested and the ground is becoming exhausted, these trees are allowed to grow up again. In other cases, of species whose root systems are especially vigorous and compete unduly with crops, these trees are killed, leaving only specimens of other, useful, species; hence there have arisen the areas with scattered trees of *Butyrospermum Parkii* or *Balanites aegyptiaca*, such as are to be seen in the north of Uganda; or of *Adansonia digitata* (Baobab), in some hotter, drier, parts of Africa. In the north of Uganda there are some places where the only tree growth is of large specimens of *Ficus* spp.; it seems very probable that these also have arisen through human influence, that woodland has been cleared, leaving only mature specimens of useful trees such as *Butyrospermum Parkii* and that, when these trees died out, they were replaced by *Ficus* spp. which had started as epiphytes on them. Although many of the roots of these fig trees are close to the surface of the soil, yet crops will grow in association with them and it is not necessary to cut out the trees; furthermore, their wood is of little use for house building and is not a good fuel; and therefore the trees are retained.

Human influence on vegetation is not purely destructive: there are some species whose abundance in Uganda is due in part to planting by man. *Ficus natalensis* and allied

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species are of little use when they are dead, but are most useful trees when they are alive; their bark is used to provide cloth, the trees provide useful shade and shelter for crops; and, as large woody cuttings are easily rooted, they are often planted on farms, are used to mark boundaries and are employed as living posts for fences; many of the trees scattered over the countryside were planted for one of these uses. Similarly, the prickly *Erythrina abyssinica* is easily grown from large cuttings and is often planted in the fences around cattle kraals; many specimens and many groups of trees appear to have originated in this way.

Plants with edible fruits furnish many examples of species distributed by man. The indigenous *Borassus flabellifer*—a species abundant and widespread in tropical Africa and in tropical Asia—has so irregular a distribution in Uganda that human action, and perhaps also that of elephants, seems to be the most feasible explanation why it should grow in abundance in such diverse situations—on steep hillsides, on undulating land and in flat valley bottoms as at Seyajongo.

Some fruit trees, which are known to be of recent introduction, have now become naturalized in many localities in Uganda—notably the mango (*Mangifera indica*) and the guava (*Psidium guajava*). The passion fruit, *Passiflora edulis*, a strong semi-woody climber, which probably was not grown in Uganda until less than fifty years ago, is now abundant in the wetter forests to the north and west of Lake Victoria: it was brought in by man, but it has been spread by monkeys and fruit-eating birds, notably parrots and hornbills.

Many succulent plants are distributed and increased by human action in Uganda. The large tree *Euphorbia calycina* and the smaller *Euphorbia Tirucallii* are used to form living fences around cattle kraals and often these fences persist long after the kraals are abandoned. Some smaller plants, especially succulents, are cultivated for medicinal purposes in regions far from their home: for example, *Stapelia Dummeri* was described from cultivated plants in Buganda, yet the nearest district where it has been seen in the wild state is Karamoja, 300 km. to the north-east; and *Kalanchoe abyssinica*, which is widely grown in Uganda, does not seem to be truly wild in any part of the protectorate. The succulent *Sansevieria Dawei*, another species first described from cultivated plants, is planted for fibre in areas remote from the dry districts where it grows wild.

The species enumerated above are some which are deliberately planted. There are others which are not abundant except as weeds of cultivation, especially the ephemeral species for which there is no place in a closed forest or in a tall natural grassland. Two exotic species—*Galinsoga parviflora* and *Euphorbia heterophylla*—which are both native to America, are striking examples of this type for, although they are known to be recent introductions, yet they are now widespread in Uganda.

The elephant grass (*Pennisetum purpureum*) which covers such large stretches of the countryside, seems to be secondary to human influence and especially to cultivation and farming. If the grass is not burnt for a few years, it is invaded by the seedlings of trees which, in course of time, would shade it out, so that the land would revert to closed forest or open woodland. The persistence of the grass therefore is due to the fact that it is usually burnt once or twice a year; if the grass is not burnt for two or three years and then becomes ignited in dry weather, the intense conflagration which results will scorch and kill most of the trees among it. Fire also appears to facilitate the establishment of the grass; after the burning of patches of *Imperata cylindrica* on the Kawanda Research

Station, the land has become colonized by *Pennisetum purpureum*; unburnt patches of *Imperata* have not been colonized by elephant grass to the same extent, but by large shrubs—*Flueggea virosa*, *Phyllanthus guineensis* and *Bridelia micrantha*—which represent a stage in the regeneration of closed forest.

Many of the papyrus swamps in valleys also seem to be secondary. *Cyperus Papyrus* is abundant in parts of Lake Victoria and Lake Kyoga, growing along the shores and forming a floating mass over the water of some sheltered bays: it is also dominant in many river valleys, well above the levels of the lakes. Papyrus was recorded in the catenas at Mpambire and Kawanda; in both places it was noted that the forest was advancing into the papyrus, so it might be expected that, when the vegetation had reached the climax, the papyrus swamps would largely have reverted to forest. It was also noted at Kawanda that the papyrus was advancing into the swampy *Miscanthidium violaceum* grassland.

The spread of papyrus upwards seems to be due to the nature of its roots, which form a spongy mass, very retentive of water and impeding its flow, so that the water table tends to rise above the place where the papyrus is growing and to make more ground swampy and suited to the plant. The rise in the water table also leads to the flooding of areas of valley grassland, so that their herbage changes from *Cymbopogon afronardus* to *Miscanthidium violaceum*, which in its turn is invaded by *Cyperus Papyrus*.

On this hypothesis, which is supported by local tradition that papyrus swamps in some places have increased within living memory, the dominance of *Cyperus Papyrus* may be regarded as a phase of the cycle:

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                    ┌─────────────────→Forest───────────┐
                    │                                    ↓
                    │                                Cultivation
          Cyperus Papyrus swamp                          │
                    ↑                                     ↓
          Miscanthidium violaceum          Cymbopogon afronardus
               grassland        ←───────── .    grassland
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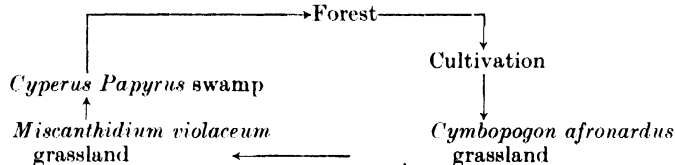
If it were not for human influence, the climax forest would have persisted; and human influence seems to retard the return to the climax vegetation, for the fires which sweep over the swamps in dry periods do great damage to the woody growth along their edges.

Finally, there are some very interesting plants which appear to be indicative of former human settlements; they may be encouraged by some alteration of the physical structure of the soil, but it is more probable that the reason for their restricted distribution is due to the extra supplies of bases—the residues of ashes from fires and of refuse from food—which accumulate in the soil near dwellings. *Dicrostachys glomerata* is a small tree or a large shrub, found on such places in the drier areas of Uganda; it was noted on the hilltop at Seyajongo. *Acacia Holstii* is often associated with old kraal sites, in regions of light and medium rainfall: it was noted on the hilltops at Kakinze and Seyajongo, and in the valley grassland at Kawanda.

Even the most important timber tree of the protectorate, *Chlorophora excelsa*, appears to be largely confined to house sites or to termite mounds on land which has been cultivated (Thomas, 1942a); almost all of the young trees to be seen in Uganda are in such situations, in places where the soil is rich in bases; and, when the tree has been planted on poorer soils, its growth has been slow. There is evidence that *Chlorophora*, which is a typically West African species, is spreading in some of the drier parts of Uganda, such as the Lango district, north of Lake Kyoga, being always restricted to settlements. And

it is most probable that the restricted occurrence of the species is the reason why *Chlorophora excelsa* trees are preserved and are the subject of many religious beliefs both in West Africa and in Uganda; the Baganda used to think that the spirits of their ancestors gathered in the shade of the trees.

THE INFLUENCE OF MAN ON SOILS IN UGANDA

The catenas at Bujumba and Nansagazi, the two most southerly of those described, are situated on rocks of the Karagwe Ankolean system, which is composed largely of phyllites and quartzites. The other four catenas are situated on the Basement Complex of schists, gneisses and crystalline quartzites; a gneiss is exposed on the hilltop at Kakinze and a ridge of quartzite at Kawanda.

There are no volcanic or basic rocks in these catenas, yet there are great differences between the soils found on them. In general, the soils to the south seem to be more acid than those to the north; as there is a heavier rainfall in the south, it might be expected that the soils there would be more leached and poorer in bases than those of the drier areas in the north. But, even in any one catena, there are great differences between the soils in different zones—in reaction, in texture and in colour. As chemical analyses are available of the Bukalasa catena (Martin & Griffith, 1940) which resembles that at Kawanda, one or two points which these catenas have in common may be mentioned.

One of the most interesting features of both catenas is the difference in the colours of the soils—those of the hilltops are grey, those of the hillsides are red brown, and those of the valleys are grey. It is a common practice to speak of all red or red-brown soils in the tropics as being laterized but, as Martin & Griffith point out, it is better to speak of the red soils at Bukalasa as 'red earths' for they have a silica/alumina ratio of about 2·0 and are on the borderline of the true laterites.

The classical work of Harrison (1933) in British Guiana showed that under equatorial conditions, with high temperatures and heavy rainfall, it is to be expected that basic rocks will weather to form laterite and acid rocks will weather to form kaolin. Kaolin appears to be abundant in the grey soils of the valleys at Bukalasa and Kawanda and also in the grey soils of the hilltops; yet the soils on the slopes between are red, and it would be difficult to account for these differences as due to ordinary soil-forming processes.

Native tradition states that the reddening of the soil is due to lengthy human settlement. This is the most feasible explanation of the change in colour, for it seems impossible otherwise to account for the occurrence of patches of reddish soils in close proximity to grey or black soils, sometimes on the same contour of the hill. Such occurrences may be seen not only in the part of Buganda described in this paper, but in many other areas of the Uganda Protectorate, in places which differ greatly in their rocks and climates.

Human settlement does undoubtedly lead to a local concentration of bases in the soil; comparisons between samples 1 and 2 at Bujumba and between samples 2 and 3 at Kakinze show that there is a much greater amount of bases in the soil near the houses than in the soil at a little distance from them. This concentration of bases is a matter of some economic importance; for example tea, a calcifuge, will not grow on old house sites; and it is a persistent effect, for the failure of tea in patches has shown the existence of house sites even in the Kijura area (in the west of Uganda) which is known to have been uninhabited for over forty years.

It is quite probable that the reddening of soil may be connected with the addition of bases. Harrison (loc. cit.) showed that when acid rocks weathered, there is a tendency for the iron to be leached out, leaving a light-coloured soil rich in kaolin; but that when basic rocks are decomposed the alkaline solution tends to remove the silica, leaving the iron and alumina, and a reddish soil is formed. Similarly, it is possible that the more alkaline soil solution, induced by the addition of ashes, of animal and vegetable refuse to the land near houses, may lead to a leaching of silica and an accumulation of iron, producing the 'red earths' so abundant in Uganda. The mounds of many species of termites are redder than the soils or the subsoils on which they are built; as in the case of human settlements, so also in the case of these mounds, it is possible that the change in the colour of the soil may be connected with the local concentration of bases by biological activity.

Whatever may be the chemical processes involved in the formation of 'red earths' in Uganda, there is much evidence of the physical processes—that often they are built-up soils. Much attention has been paid to erosion of tropical soils, but little to the processes by which they are built up. Soil erosion does occur in Uganda, but is much less evident in Buganda than in the Eastern Province, where the soils are more sandy and the dry seasons more marked. The more spectacular examples of soil erosion in the tropics are not usually to be seen in the areas of heavy, well distributed rainfall, where a cover of vegetation is maintained over the soil; but they are to be seen in places where the total annual rainfall is less and where the dry seasons are so long that most of the plants are grazed or burnt away, exposing the bare soil to the full force of the rains when they break.

Even though there may be little erosion of the soil surface in Buganda, it seems that there is a definite movement of the soil downhill, a movement which gives rise to the popular superstition that the stones on the hilltops grow in size. It is probable that this movement is due to 'soil creep'—the slow movement of the particles underground when they are wet—for, while the construction of narrow-base contour bunds in coffee plots at the Kawanda Research Station has effectively prevented the movement of water or soil on the surface, yet it has led to a rapid terracing of the land.

The diagram of the catena at Kawanda indicates that there has been a movement of soil from the hilltop. The level of the land falls steeply down to the area which is cultivated; it falls more slowly throughout the inhabited part of the hillside, and then falls rapidly again, from below the lowest houses, down to the almost flat valley bottom. This profile is characteristic of the countryside in the densely populated parts of Uganda; even the lower hills, on which a rocky outcrop is lacking, have gentle slopes from the top to a long way down the sides, and then fall rapidly to the floor of the valley. The shape of the valleys cannot be attributed to erosion by the slow currents of water which percolate along them through forests or papyrus swamps.

It is more probable that the shape is due to the fact that, where the dwellings are, there the soils tend to be built up. That seems to be the most feasible explanation of the very deep deposits of even-textured red earths. Furthermore, there is much evidence that these soils have been and are being built up fairly quickly in some places: it is a common experience to see potsherds at depths of half a metre or more, even on hilltops; and, as the local pots are seldom very thoroughly baked and tend to disintegrate rapidly in moist soil, it is probable that these fragments are of no great age.

Evidence that the occurrence of red earths may be correlated with former human settlement is by no means confined to Buganda. It is plainly shown in some of the drier parts of Uganda and other East African territories and is easily seen from the air; the patches of red soil in some cases end abruptly, in other cases the colour grades into the paler shades of the land around. The patches of red earth are in places where supplies of water are available, or where it is probable that water has been available, and are usually on slopes well above the water table.

Much has been written about human influence on soil erosion in equatorial Africa; but there has been little mention of its function in building up soils in that region. Yet this accretion of soils on the sites of settlements is well known in other parts of the world; it is obvious in the case of many cities in Europe; and it is shown even more strikingly by the deep deposits of alkaline soil covering the remains of former civilizations in Egypt, in Iraq, and in northern India. If human settlement has caused the building up of soil in other parts of the world, it might be expected to do so in the tropics; and it seems to furnish the most reasonable explanation of the facts detailed above.

LATERITIC IRONSTONE

The origin of lateritic or red soils is a controversial subject; the origin of lateritic ironstone and lateritic gravel is even more controversial. Mackay (1943) has compiled an account of many theories on this subject. His observation that exposures of laterite frequently occur near old village sites in forest country and are probably quite a good indication of former forest clearance and cultivation is most interesting, and accords with the conclusion which had been reached after many observations in Uganda. Lateritic ironstone and lateritic gravel are common in the Protectorate and occur at many levels, on many rock formations, and under a wide range of climates—from the wettest to the driest. Outcrops of ironstone are found under a wide range of conditions, but the recent deposits have one feature in common—they are in places where it is probable that there have been human settlements. A major factor in determining human settlement is the supply of water, and it is very striking how often these outcrops are in places where water is available, although they are usually well above the present water table.

It has been suggested that lateritic ironstone has been laid down under water or on the shores of lakes or in places where there is a seasonal fluctuation of the water table; but there has been noticed no evidence of the formation of a layer of iron concretions in any such position at the present time on any of the hillsides described in this paper. And ironstone is abundant at many different levels; on the Sese Islands and on the shores of Kyagwe it occurs at the summit of the peneplain, but it is usually at lower levels in the north; and, even on a single hillside, as at Nansagazi, it may occur at several different levels. The discontinuous distribution of lateritic gravel, which appears to be derived from lateritic ironstone, is well shown on the Kawanda Research Station; one end of the hill has red soil and much lateritic gravel, and the other end has shallow grey soil around an outcrop of quartzite; there are patches of gravel irregularly disposed on either side of the hill, not on the contour, but extending for some distance down the slopes.

And it has been suggested that ironstone may be formed by the rising of the soil solution; if this were the case, it could be expected that the outcrops would be horizontal, i.e. parallel to the water table in the soil. But the outcrops are not always horizontal—often they are on a distinct slope, parallel to the surface of the ground. So that it seems more

likely that the formation is due to concentration of the solution, as it percolates downwards, through meeting an impermeable layer; this would explain the incrustation of ironstone on rock surfaces. In the cases where the ironstone is formed in the absence of rocks, the impermeable layer may be the hard pan which often results from native cultivations—the soil being turned over to the same depth time after time - or by the compaction of the soil on which dwellings have been built. There is very little lateritic ironstone or lateritic gravel in places where the soils contain much coarse sand as, for example, those derived from granites in the Mubende district (to the west of the area described in this paper); however much these soils are compacted, they remain very permeable. Encrustments of lateritic ironstone are often to be seen on quartzites in Uganda, but not on granites.

One strong argument that ironstone is formed through some human influence is the manner in which both solid lateritic ironstone and lateritic gravel are found in patches even more localized than the red earths. It seems impossible to account for this sporadic occurrence, except through human agency. It certainly cannot always be attributed to the distribution of rocks; the unconformity of rocks and of lateritic ironstone and gravel may well be seen on the cuttings of a new road between Sipi and Sebei, on the north-west of Mount Elgon; these cuttings would afford valuable material for an intensive study by a soil chemist.

Some of the most striking examples of lateritic ironstone are to be seen on the promontory of Entebbe, and other headlands projecting into Lake Victoria, where the deposits are very deep: there is usually a shallow layer of lateritic gravel, then a hard layer of ironstone and then a softer, mottled mass to a total depth up to 8 or 10 m.; in some places the softer lower layers have been eroded, leaving the hard upper layer to form a cave or a natural bridge. The distribution of these masses of ironstone is very irregular—they are usually well developed on the headlands, and are usually absent in the bays. One of the most interesting occurrences is near the end of the Entebbe promontory, which runs towards the south-west—there is a line of regularly spaced outcrops projecting into the lake in the direction of due south. It seems scarcely credible that these outcrops can be due to 'natural' causes; and, if they are due to human settlement, it is interesting to speculate why they should be thus arranged. Similarly, the circular outcrop of Nansagazi seems hard to explain on 'natural' grounds.

There appears to be no native tradition that outcrops of ironstone are to be associated with human settlement, as is the case with the reddening of soil. But it is a significant fact that the spot which used to be most sacred to the Baganda, the site of the temple of Mukasa, their principal deity, was an extensive sheet of ironstone on Bubembe Island in the Sese group; for Mukasa, like the other gods of the Baganda, appears to have been a deified person, and the temple was built on the site of his dwelling.

Finally, one great argument that ironstone may be built up through human interference is the fact that it tends to diminish through natural causes. First, it is eroded rapidly by water, as is shown by native tradition; ironstone causeways which connected islands in the Sese group are now deep beneath the lake; the rock Sali at the south side of Bunjako Island, which was connected to the mainland by a strip of ironstone, is said to have floated away. Secondly, there is evidence that, when an ironstone pavement or lateritic gravel is under a forest cover, it tends to disintegrate, a process which may be seen on the Sese Islands, where trees grow well on such pavements (Thomas, 1941)

and which has been noted in Nigeria (Rosevear, 1942) and on the Ivory Coast (Porteres, 1937).

There are considerable areas of ground in some densely populated parts of equatorial Africa which are rendered infertile by layers of lateritic ironstone. If, as seems probable, these layers can be broken up by forest growth and the land rendered fertile again, such a process would be of great economic value; the processes by which the ironstone is built up and broken down seem to demand intensive study. It is possible that the processes are much more rapid than would be expected: at Nansagazi and on some of the islands near the north of Lake Victoria there may be seen cases of *Chlorophora excelsa* trees growing in crevices of ironstone pavements; as *Chlorophora* is a long-lived species and one that demands high soil fertility, it is possible that the ironstone has been exposed, or even has attained its present hardness, after the trees became established.

THE ANTIQUITY AND DENSITY OF HUMAN SETTLEMENT IN UGANDA

If such far-reaching changes of vegetations, of soils, and even of rocks are to be attributed to human influence, it is essential that there must be proof of long-continued human settlement in the country. Such proof is now available: Wayland (1934) has shown that not only can the same sequence of stone-age cultures be traced in Uganda, as are known in Europe, but also that there was a far greater density of settlement here. In his M horizon in the valley of the Kagera River there is a layer composed entirely of artefacts, embedded in a mass of lateritic ironstone. The horizon provides more evidence that ironstone may be connected with human settlement; similar tools are to be found in reddened earth of Bed 2 at Oldway in Tanganyika; the reddening may be caused by a change in climate but, by analogy with present-day conditions, it is possible that it was due, at least in part, to dense human settlement.

Life is easy on the northern shores of Lake Victoria. The climate is never very hot, never very cold, never very wet and never very dry. As the rainfall is so well distributed, a supply of food is relatively easily maintained, far more easily than in temperate regions with a long cold winter, for crops may be harvested at all times of the year and fish and game may be obtained at nearly all seasons. Clothing is unnecessary, and housing may be of the simplest. It is only to be expected that primitive man, with a minimum of tools, should flourish and multiply here to a far greater extent than under more rigorous climates.

It seems that even fairly recently the population of the Uganda Protectorate was much greater than at the present time. Roscoe (1911) states that about 1860 the population of Buganda alone was about 3,000,000; now, although the area of the province has been increased, yet the population is only about 900,000. There was a tremendous wastage of population in the years before British rule commenced, a wastage due to wars, to famines, to disease, and to the human sacrifices and executions which seem to have accounted for thousands of victims each year.

Furthermore, if striking effects are to be produced on the soils, there should be long continued human settlement in certain places. It is quite probable that large settlements *would be made and continued on the islands and headlands on Lake Victoria*, for the inhabitants of such settlements could resist attacks from their enemies. In dry areas, there might be permanent settlements close to supplies of permanent water—the rivers and waterholes which did not dry up at any season of the year. But, in a well watered area like the south of Buganda, it should be possible to change settlements at frequent

intervals; and so long as cultivation was in the primitive form of cutting down the forest, taking a few crops off the soil until it lost fertility and then moving on to fresh areas, so long as this system of agriculture continued, no permanent settlement could be expected.

But permanent settlements, based on the cultivation of a perennial crop, the banana, appear to have been a feature of Muganda life for a long time. There is often a connection between the antiquity of a crop and its religious significance; and, as Roscoe shows, it was the banana crop on which the life of the Baganda was centred, the crop with which the ceremonies of birth and death were connected, which was used to give protection from sickness and which supplied offerings for their gods.

Yet the banana is not an African plant; it originated in south-east Asia; it sets no seed and can only be grown from suckers, heavy pieces which the African would be unlikely to carry for many miles. Nevertheless, there were over thirty varieties of banana in Uganda before the coming of the Europeans: a few may have arisen by bud mutation, but the majority must have been introduced. If climatic conditions at the time of intro- duction were like those of the present day, it is unlikely that the bananas were brought to Uganda from the east, north or west: the southern route, down the western side of Lake Victoria, the rift of Lake Tanganyika and the Zambesi valley to the coast, seems to be the most likely, for it alone provides an uninterrupted stretch of inhabited country suited to banana cultivation. An even greater mystery than the manner in which so many varieties can have been brought all the way from the coast to the centre of the continent is the manner in which the bananas reached Africa at all—were they brought by the Portuguese, or by the Arabs before them, or by the Chinese, who appear to have been the first people to carry on a regular trade by sea with Africa?

However the bananas may have reached Uganda, there is no doubt that they have been cultivated to the north of Lake Victoria for a very long time and on a very extensive scale. The bananas are deep rooted plants and respond greatly to soil fertility—they will not grow on poor soils; so the African plants his banana garden on the best available land and builds his house in it. The ashes, the refuse of food and the manure from stock tend to accumulate near the house, maintaining and increasing the fertility of the soil, so that a well-kept banana garden may persist for a hundred years or more. On poorer soils, the life of a banana garden will be much shorter and the land must be left for a spell under a fallow of elephant grass or of a secondary forest before it recovers sufficient fertility for another crop of bananas to be grown. Even if the banana gardens have a short individual life, yet there is a tendency for them to be replanted again and again on the same piece of land and there is a tendency for plant nutrients to accumulate in such areas; whereas the land nearby which, if it is under forest is used to provide firewood or, if it is under grassland is used to provide grazing and thatching material, tends to become further depleted of its nutrients. Thus there may be produced the striking differences of soil fertility between the zones on any one hillside.

THE INDIRECT EFFECTS OF HUMAN INFLUENCE ON VEGETATION

It has seemed necessary to digress from botany into the more controversial sciences of anthropology and soil science in order to appreciate the indirect effects of human influence on vegetation. For the direct effects may produce temporary changes; but the indirect effects may produce permanent changes. If a field of grassland is burnt, it may be expected that the grasses will spring up again in the next rainy season. But if a forest is

felled, and the land is cultivated and exposed to the deleterious action of sun and rain for a long period, the mineral status of the soil may be so much lowered that the woody species cannot regenerate and open grassland replaces the forest.

Any disturbance of the natural cover of the soil is likely to increase the rate of leaching and the ultimate loss of plant nutrients; it would be interesting to analyse the waters of the River Nile and to calculate the amounts of various salts which are carried down each year from the Lake Victoria basin to fertilize the farmlands of Egypt. But human influence is not always destructive of soil fertility; just as the farmlands of western Europe are probably now much better supplied with plant nutrients than when they were under temperate forests (especially in the case of areas which were under coniferous forests) so also it is probable that the soils of the banana gardens in Uganda have now a higher mineral status than when they were under tropical evergreen forest.

Yet it is probable that the mineral status of the grassland soils has been lowered and is still being lowered; the salts taken up by the grasses are carried away by the animals which graze on them and a high proportion is not returned to the grasslands, but is deposited on the spot where the animals are kraaled at night. As the mineral status of a soil is diminished, the composition of its herbage changes (Thomas, 1940). In those parts of Uganda which have a well-distributed rainfall, *Pennisetum purpureum* grows on the richest soils, *Cymbopogon afronardus* on those which are poorer and *Loudetia kagerensis* on the poorest of all.

The change in the composition of the herbage appears to have a great influence on the surface soil, not only as regards its structure, but also as regards its mineral status. A large collection of grasses has been planted at Kawanda Research Station on fairly good soil: it has been found much easier to establish species such as *Pennisetum purpureum* and *Cynodon plectostachyum*, which grow on good soils, than to establish species such as *Eragrostis chalcantha* and *Loudetia kagerensis*, which grow on poor soils. The reason seems to lie in the differences between the root systems of the grasses: as a general rule, the species which grow on good soils have vigorous, deep, roots, but the species which grow on poor soils have weak, shallow, ones. Therefore if it is only possible for these latter species to grow, the minerals in the deeper layers of soil and subsoil are much less available to the herbage than if more vigorous species are growing, and it may be expected that more of the salts will be leached out by percolation of soil water. The *Loudetia kagerensis* grassland on the hillside at Bujumba furnishes an example of such a soil: it is very permeable and is of great depth, and yet the grass roots can draw upon only the leached upper layers. The seedlings of trees are unable to become established in this poor soil, except close to termite mounds where the mineral status of the surface soil is higher.

Whenever forest does not invade an area enjoying an equable temperature and a good well-distributed rainfall, with no water-logging, it is usual that the poverty of the soil is an inhibiting factor. This poverty may be due to the fact that the soil has been leached before it is deposited, in which case podsolization may take place, even under tropical conditions (Richards, 1941); such deposits may be seen near Lake Nabugabo in the Masaka district, in the south-west corner of the area included in the map (Thomas, 1942*b*). Yet it seems that instances of such poor natural soils are not very common in the tropics and that most of the areas of permanent grassland in close juxtaposition to tropical evergreen forests are due to soil degradation by human influence.

And so it seems that by removal of the nutrients from some zones and their concentration

in others, a pattern of soils differing in colour and in mineral status has been built up, such that the most fertile soils are often to be found on the tops and sides of hills, and not near their bases, as would be expected from ordinary soil-forming processes. This diversity of soils is reflected in the diversity of vegetation, with communities differing greatly in composition and life form, instead of the more uniform vegetation which probably existed before the coming of man.

Not only do the soils differ greatly in mineral status from zone to zone, but also there are great local variations inside the zones. Termites and some mammals, which tend to place their excreta in certain spots, may cause local accumulations of plant nutrients; but it seems that most of the variability of the soils must be ascribed to human influence.

THE COACTION OF MAN AND VERTEBRATE ANIMALS IN UGANDA

If, as seems highly probable, the wetter part of the Mengo district was at one time covered with dense evergreen forest and owes its diversity of plant formation to human influence, it is interesting to speculate how the change of plant population has been reflected by a change in the animal population.

Even the animal populations of the lake waters have been affected. In spite of all the fishing in the waters of Lake Victoria and Lake Kyoga it is probable that the fish populations have not been greatly altered, except in the case of the most desirable *Tilapia esculenta*. But many crocodiles are shot each year, and their numbers must be reduced. The hippopotamus, and the situtunga, an antelope living in swamps by the shores of the lake, undoubtedly are much fewer than they would be in the absence of man.

If continuous forest covered the northern shores of Lake Victoria, it might be rich in monkeys, fruit-eating bats, squirrels, tree hyrax, giant forest hog and blue duiker. The large mammals—the bushbuck, the buffalo and the elephant—all of these would be encouraged by clearing of patches of the forest, for they prefer the combination of closed forest and open grassland or woodland. Many of the other antelopes, the zebra and the wart hog, all of which like short grass country, these would be encouraged by human influence in cutting down forest and woodland and in keeping the grass short by annual burnings. And these larger animals have a great influence on the pattern of human settlement in the less populated areas, for they may do so much damage to crops as to render cultivation unprofitable. The inhabitants of small, isolated settlements often give up the struggle against the ravages of elephant, of buffalo or even of wild pig, and take up their abode in more densely settled areas, from which the animals have been driven away.

The bird population of this countryside is exceptionally rich both in numbers of species and of individuals; human influence, by inducing a pattern of forests, grasslands, cultivations and settlements, a pattern so well suited to a diversity of birds, undoubtedly has encouraged many species. If the area near the lake had been under continuous forest, it would no doubt have been rich in species suited to forest conditions—parrots, plantain eaters, hornbills, pigeons and warblers. But the man-made cultivations and grasslands have provided food and territory for many other groups which live in open country or which feed on grass seeds, groups like the doves, the finches and waxbills, the widow birds and sunbirds. And the density of settlement has encouraged other species which flourish near human dwellings—sparrows, swallows, wagtails and weaver birds. As there is now such a diversity of plant communities on any one hillside, so there is also a great diversity

of bird communities; the birds of forests, the birds of grasslands and the birds of habitations are all to be found on a single hill.

THE COACTION OF MAN AND INSECTS IN UGANDA

Mention has been made of the fact that the Mabira Forest in the east of the Mengo district has sprung up in an area where settlement is discouraged by the *Simulium* fly which breeds in the River Nile. This is a minor example of the way in which the distribution of human population is influenced by that of insects.

The tsetse flies, which abound in so many parts of tropical Africa, are a most important group in this respect, for the trypanosomes which they carry have killed out the populations of men and of cattle from many areas. The fly belts are not static; they advance and retreat and their cumulative influence on settlement and grazing and, in consequence, on vegetation, is impossible to assess. One minor instance of this influence is to be seen in the recent loss of stock at Seyajongo. The tsetse flies have an indirect effect as well, for it is known that their spread is retarded by grass fires, a method of control widely used by African tribes and which tends to prevent the regeneration of trees.

Even the distribution of the honey bee has had a great influence on African vegetation, on account of the fires lit to smoke the bees out when honey is gathered. This effect can be seen far from the limits of human settlement, especially on the mountains, where the fires have produced great changes in the vegetation. It seems that fires have induced grasslands in place of the original shrubby vegetation of mountain moorlands (Thomas, 1944), and fires have also destroyed huge stretches of mountain forest. There are belts of upland bamboo (*Arundinaria alpina*) on some mountains in East Africa, while on others the plant is absent. The most feasible hypothesis to account for the distribution of this species is to regard its growth as secondary; that, just as a thicket of elephant grass will take the place of forest at an altitude of about 1100 m., so also a thicket of bamboo will take the place of forest at an altitude of about 2200 m. The hypothesis is supported by the way in which the forest spreads into the bamboo and shades it out.

Termites are undoubtedly a very important group in tropical ecology. They destroy much plant material but, by their action in concentrating nutrients, they render it possible for woody growth to start in places where, without them, the soils would be too poor. They have a great influence on human life, for they rapidly destroy many human dwellings and new ones must be built. But, when the termites swarm at the beginning of the rains, they are collected in large numbers for food and are greatly relished; and on this account their mounds are not often destroyed. The construction of motor roads seems to favour *Termes bellicosus*, as the banks beside the roads are chosen as the sites for mounds, which are built up at frequent intervals, sometimes so close as to produce an architectural effect. Roads, as well as cultivations, have a great influence on tropical ecology: they act as barriers to grass fires and they encourage the movement of animals, and especially of some insects such as tsetse flies.

The best known coaction between insects, disease and man is, perhaps, the spread of malaria by mosquitoes, and it is recognized that this spread has had a great influence on history, not only in the tropics, but in temperate countries as well. Mosquitoes are abundant in Uganda, and malaria is prevalent. The Baganda did not connect the fever with the insect, although they did know that there were different strains of the disease and that a man who might be immune to malaria in his own home was liable to develop

fever in another district—a fact which was attributed to the drinking of water from another river. (It seems that the connexion between malaria and mosquitoes was long known on the Somaliland coasts, for Burton (1856) records in a footnote: 'The mosquito bites bring on, according to the same authority (the Somalis), deadly fevers; the superstition probably arises from the fact that mosquitoes and fevers become formidable about the same time'; that was written about forty years before the connexion was proved by Ross.)

Although the Baganda did not know that mosquitoes carried malaria, yet they avoided the insects because of the annoyance they caused; it is mentioned in the discussion on Bujumba catena that the Sese people built their houses on the hilltops to avoid the mosquitoes by the lake. For the same reason, the houses on the mainland were built on the hills; even in places where there were no swamps in the valleys, mosquitoes could breed in the water standing in deep hoof marks on the valley grasslands; so the Baganda dwelt on the sides or tops of the hills, although that entailed more labour to carry water up the slopes. One catena described shows an exception to this rule—that at Nansagazi— but this appears to be the exception which proves the rule, for there is a strong land breeze during the night at this place and mosquitoes are scarce even near the shore of the lake.

No other reason for the choice of dwelling sites on hills is put forward by the Baganda: the low hills were of little use for defence; and there was no question of endeavouring to get a good outlook, for the houses were almost always arranged to face the hillside, with their backs to the view. Only one class tended to live in the valleys—the herdsmen, in whose kraals and huts very smoky fires were maintained to keep flies away from the stock; the cows stood in smoke so that they could keep quiet while being milked; and this same smoke would drive away the mosquitoes.

It therefore seems that the pattern of human settlement in Uganda has been largely determined by the prevalence of mosquitoes, and that, because the people were driven to settle on the sides and tops of hills, the soils became enriched there, rather than near the base of the slopes as would be expected from the climatic causes of soil formation. And, as shown above, the pattern of soil fertility has influenced the pattern of vegetation. These actions, reactions and coactions between insect, man, soil and plant furnish a good illustration of the necessity to regard the plant-animal formation as the basic community unit (Clements & Shelford, 1939).

The importance of human influence in tropical ecology

As it has seemed necessary to describe both the vegetation and the soils in some detail in order to show what differences occur in a small space, it has been necessary to confine the description to six hillsides in a small area of country. But many of the phenomena recorded here have been noted in other countries: for example, the occurrence of red soils and black soils in close proximity, where no obvious reasons for the differences in colour are visible, has been recorded from Tanganyika (Milne, 1936), from South Africa (Marchand, 1924) and from India (Raychaudhuri, 1941). Similarly, the arrangement of soils in a catena in the Nigerian cacao belt, described by Vine (1941), has much resemblance to that seen in Uganda. The diversity of theories about the formation of lateritic iron-stone in many countries shows how difficult it is to explain its occurrence on climatic or topographical factors alone. The red earths of Uganda are more fertile than the 'laterized' soils of some other countries near the equator, especially those with heavy

rainfalls where the soils are badly leached; but it is probable that there has been the same cycle—forest, cultivation, forest—over many hot, wet areas; and it is probable that, in many places, the cycle has been repeated again and again.

The size and complexity of the ancient buildings in Central and South America, in Ceylon and in Indo-China are evidence of the civilizations which have flourished near the equator. There are no such spectacular ruins in equatorial Africa but, even in Uganda, there is evidence of a highly organized society in times past—the present day African is unlikely to have built the earthworks at Biggo or the dams at Ntusi (both places lie in the Masaka district, south-west of the Mengo district). Such large remains are scarce and in other places the evidences of man are less easily perceived—there may be a few worked stones, a pit dug for iron ore, some slag from iron smelting, a grindstone or some pieces of broken pot; and, as mentioned above, the pottery is often recent, as much of it disintegrates quickly in the soil.

But, in many parts of Uganda, even these slight indications of human activity are missing; the evidence must be sought in the vegetation and in the soil itself. The secondary nature of the vegetation even in forest areas is strong evidence of past interference; Eggeling (1940) has shown that little of the Budongo Forest has reached the *Cynometra Alexandrii* climax, and that the forest is spreading rapidly. The Mabira Forest is even younger, as is shown by the high proportion of the short-lived, soft-wooded trees; and the soil itself provides evidence that it has been greatly altered by human activities, evidence depending not only on its red colour, but also on the way in which it has been scored with deep gullies, such as could not have been formed under a forest cover, and the way in which differences in soil reaction are localized, acid and alkaline soils being found in close proximity. There seems to be an interesting correlation between soil alkalinity in the Mabira Forest and an abundance of *Dracaena fragrans* in the undergrowth, for this *Dracaena* is much used as a hedge plant near dwellings and it is probable that it has persisted in the forest long after the houses have gone. There is a great contrast between the young Mabira Forest, the young parts of the Budongo Forest and the older forest in Bwamba, on the west of Uganda—an extension of the Ituri Forest of the Belgian Congo. This Bwamba Forest consists largely of a pure stand of rather small *Cynometra Alexandrii*, growing on a grey soil, and it is probable that it has been little altered by man.

It is very difficult to account for the present vegetation formations in Uganda and in other parts of equatorial Africa, unless allowance is made for the effects of human influence in many places. Michelmore (1939) has tried to explain the distribution of open grasslands in Africa on the assumption that they are primary formations and has evolved ingenious explanations as to why the grass grows often on deep flat soil, while the forest is on rocky steep places. It appears much simpler and more logical to regard the vegetation of equatorial Africa in the same light as Cook (1909) regarded the vegetation of Guatemala: 'The driest and most sterile localities, those too forbidding for human occupation, have retained their forest growth, scarcely excepting sheer precipices and exposures of bare rocks. The regions which are now treeless and barren or covered only with grass are those naturally well suited to the growth of forests, for the formation of fertile soil and for human occupation. Indications of prehistoric agriculture are found in all the desiccated areas, as well as in other regions now covered with forests. The abundance of rubber and other temporary types of trees and the absence of humus-inhabiting

arthropods and forest palms enable regions of recent reforestation to be distinguished from forest of older growth. Facts of several different kinds thus support the conclusion that the Central America region had a continuous forest covering before the advent of agricultural man. If human interference were withdrawn, the normal growth of the vegetation would again cover the Central America region with dense and continuous forests.'

There seems to be a very close parallel between conditions in Guatemala and conditions in Uganda, even to the abundance of rubber-producing plants in the younger forests; for a wartime drive for rubber production has shown that both the wild rubber trees (*Funtumia elastica*) and vines (*Clitandra orientalis* and *Landolphia* spp.) are characteristic of certain phases of forest regeneration.

Plant growth is very rapid in warm and wet regions and there has been a tendency to regard any forest of large trees as of great age, and even to say it is 'virgin'. But there does not seem to be much virginity left in most parts of equatorial Africa, for little of the vegetation is in the climax stage.

The European conception of Africa is largely founded on the writings of explorers and, of these, Stanley's books had a great vogue. Stanley visited Uganda twice and described his travels in *Through the Dark Continent* and *In Darkest Africa*; and he wrote in a strain to match the titles. But even Stanley had to convey to his readers how much of the country was cultivated—he thus described the countryside near Kampala on his first visit in 1875: 'Beautiful landscapes were thus enjoyed of rolling lands and placid lake, of gigantic tamarinds and gum-trees, of extensive banana groves and plantations of the ficus, from the bark of which the national dress, or mbugo, is made.' (Stanley, 1878.)

Speke, who visited Uganda thirteen years before Stanley, wrote thus of the vegetation in 1862: 'The broad road, like all in Uganda, went straight over hill and dale, the heights covered with high grass or plantain groves, and the valleys covered with dense masses of magnificent forest-trees surrounding swamps covered with tall rushes, half bridged' (Speke, 1863).

Grant (1871), who accompanied Speke, wrote of Uganda: 'These ridges and mounds of rock and clay are of a uniform height, their flat tops are covered with a woody reed, 10 feet high (*Pennisetum Benthamii*): their sides are boulders in red clay, a few trees appearing amongst the rocks: lower down field upon field of plantains and of grains mark the dwellings of the people; and at the lowest depths we have the vilest bogs, concealed by the beautiful papyrus, magnificent trees, and creepers.' This is a good summary of the hillside at Mpambire, over which Grant probably passed on his way to Kampala.

Emin Pasha (1888) made these notes on Bunyoro in 1876: 'Many fields of sesame, durrah plantations, half withered for want of rain, scattered banana groves, and many huts, at present deserted by their inhabitants, indicate a very dense population.... Many glades are seen in which tree-like Solaneae grow luxuriantly with orange, red and yellow fruits; they point to former cultivation, as do many bananas and deserted hearths.' And of his journey in the same year from Bunyoro south to Kampala: 'From village to village, or rather from beer-jug to beer-jug, we marched.' And, finally, Portal (1894) described the journey from the Nile to Kampala in 1893: 'We have been wandering through a country consisting entirely of banana groves, which took about five days to get through—miles and miles of bananas.'

It is only eighty years since the first Europeans came to Uganda, but it is known that, through all that time, a great deal of the land has been under cultivation. The plant communities have been influenced not only by climate and edaphic factors, but by biological factors as well: human influence has played a major part in determining the present vegetation of the countryside. And that is the reason why it has seemed worth while to study the ecology of such an area, for the changes which have been, and are being, produced by man are of the greatest economic importance.

Worthington (1938) has stated: 'Where agriculture is highly developed, as in most parts of Uganda, an ecological survey in the usual sense would be mainly of academic interest.' But, in order to get a true picture of Africa to-day, it is essential to consider the whole community—the climate, the soil, the plants and the animals, including man. There is a multitude of problems connected with plant ecology in Africa, problems such as the reason why so many of the trees typical of secondary forest growth should contain latex, although they belong to widely separated families such as the Apocynaceae, the Moraceae, the Euphorbiaceae, the Sapotaceae and the Guttiferae. And why, as Michelmore (loc. cit.) has pointed out, there should be swamp forests in regions of heavy rainfall, but none in the drier areas—is it a question of soil reaction, that trees cannot tolerate the alkaline soil reactions of the dry area swamps, where lime is often deposited as concretions? Or are physical factors involved, for the trees in swamps which are always wet can subsist on a superficial root system, while those which grow in seasonal swamps must have deep roots which may not be able to withstand the strains of tenacious clay soils, expanding in wet seasons and contracting in dry seasons? Human influence seems to have little bearing on such problems, but it seems to have a great bearing on the present distribution of the vegetation.

Not only is it essential to pay regard to human influence in African ecology, but also it is essential to remember that there have been great climatic changes, which have had a profound influence on life in the continent (Moreau, 1933). There is much evidence that the forests once covered much greater areas and that there was a forest belt connecting equatorial Africa with tropical Asia. Not only have there been great changes in the climate but also in the human population, for it seems that the negro element represents a fairly recent immigration from Asia. If there was a great belt of forest at the time when this immigration took place, it is possible that the bananas might have been brought in overland from Asia; this would accord with the tradition that Kintu, the mythical founder of the race of Baganda, brought the banana from the east.

The population of plants also has changed for, apart from sorghum and finger millet, the more important food crops of equatorial Africa are from other continents—bananas, sweet potatoes, yams, cassava, maize, beans and groundnuts. The cultivation of these exotics has had a great influence on the pattern of the indigenous vegetation. And, just as it is the plant communities, rather than the human artefacts, which testify to human settlement in Africa, so also it is the abundance and antiquity of introduced food plants which demonstrate the amount of contact between central Africa and the outside world, rather than the few ancient blue glass beads and the cowrie shells which give evidence of external trade.

Until about fifty years ago, slaves and ivory were the most important exports from Uganda; but now the protectorate is a prosperous country, with large exports of agricultural produce—cotton, coffee and oil seeds are some major products. And with them,

each year, there is exported some of the country's reserve of plant foods—of phosphates, of lime and of potash. While there was no export trade and while cultivation was restricted to the growing of food crops, which were consumed locally, the soils of Uganda could maintain their fertility; but now, not only are large amounts of plant food being exported, but also the land often does not revert to grassland long enough to recover its structure and fertility.

It is possible that the grass fallows will prove insufficient to control erosion as pressure on land increases and that terracing, as is done in densely populated countries of the East, will be necessary; rice, which produces so large an amount of human food per acre, may have to become a crop of greater importance in those parts which are suited to its growth. And it may be necessary to import manure on a larger scale for, as Worthington (loc. cit.) points out, the imports of fertilizers have been very small.

Ex Africa semper aliquid novae. But many new people, many new crops and many new cultures have flowed into Africa; and it is essential that the flow of new ideas and new methods should continue, in order that man may cope with the rapidly changing conditions in the continent.

SUMMARY

1. The catena system is used to describe the belts of vegetation on six hillsides in Uganda. One of these hillsides is on the Sese Islands in Lake Victoria, the other five lie between Lake Victoria and Lake Kyoga; the hills are in the equatorial belt, but the rainfall diminishes from over 2000 mm. in the south to less than 1000 mm. in the north of the area in which they lie.

2. There are great differences between the plant formations of the zones on each hill. In general, the two most southerly catenas show belts of short grassland on the hillsides, with closed evergreen forest on the tops of the hills and at the bases of the hills; the two central catenas are remarkable for the thickets of elephant grass on the hillsides; the two northern catenas have woodlands on the tops and the sides of the hills, and more or less open grassland in the valleys.

3. All of the hillsides show much evidence of past and present human influence and some of them are carrying a dense human population at the present time. As a rule, the houses and cultivations are situated on the sides and tops of hills, rather than in the valleys.

4. Short descriptions are given of the soils, and the results of simple tests on them. There is a great diversity of soils on each hillside, a diversity of colour, of reaction, and of the content of phosphate, lime and potash. The soils where the people are living and cultivating are usually redder in colour and richer in nutrients than those of uninhabited zones.

5. The secondary nature of the vegetation is discussed and the ways in which man has altered the plant formations, by cutting down forests, by burning, by the conscious or unconscious encouragement of some indigenous species and by the introduction of exotic species.

6. It is suggested that the formation of some red earths and of some lateritic ironstone may be attributed to human influence and that there is sufficient evidence of the antiquity and density of human settlement in Uganda to account for these effects; without human influence it is unlikely that plant nutrients would be more abundant on the tops and sides of hills than in the valleys.

7. The coaction of man and animals is discussed: the clearing of forests has produced conditions suited to some mammals, and human settlement has led to an increase in the bird population, both in numbers of species and in numbers of individuals. The coaction of man and insects is also discussed and it is surmised that the abundance of mosquitoes in the valleys has caused human settlement to be concentrated on the sides and tops of hills, and that it is therefore indirectly responsible for the present pattern of rich soils and poor soils.

8. Human influence is a factor of great importance in tropical ecology, and must be considered in relation to the present aspect of vegetation in equatorial regions, and to the changes which are taking place.

REFERENCES

Burton, R. F. (1856). *First Footsteps in East Africa.*

Clements, F. E. & Shelford, V. E. (1939). *Bio-Ecology.*

Cook, O. F. (1909). Vegetation affected by agriculture in Central America. *Bull. U.S. Bur. Plant Ind.* no. 145.

Eggeling, W. J. (1940). Budongo—An East African Mahogany Forest. *Emp. For. J.* **19,** 179–96.

Emin Pasha (1888). *Emin Pasha in Central Africa, being a collection of his letters and journals.*

Grant, J. A. (1871). Botany of the Speke and Grant Expedition. *Trans. Linn. Soc.* 1873, p. 5.

Harrison, J. B. (1933). *The Katamorphism of Igneous Rocks under Humid Tropical Conditions.*

Mackay, J. H. (1943). What is laterite? *Farm and Forest,* **4,** 10–15.

Marchand, B. de C. (1924). The origin of black turf soils in the Transvaal. *S. Afr. J. Sci.* **21,** 162–81.

Martin, W. S. (1944). Grass covers in their relation to soil structure. *Imp. J. Exp. Agric.* **12,** 21–32.

Martin, W. S. & Griffith, G. (1940). Uganda soils. *Agriculture in Uganda,* p. 64.

Michelmore, A. P. G. (1939). Observations on tropical African grasslands. *J. Ecol.* **27,** 282–312.

Milne, G. G. (1935). Some suggested units of classification and mapping, particularly for East African soils. *Soil Res.* **4,** 183–95.

Milne, G. G. (1936). *Report on a Soil Reconnaissance Journey in Tanganyika Territory.*

Moreau, R. E. (1933). Pleistocene climate changes and the distribution of life in East Africa. *J. Ecol.* **21,** 415–35.

Portal, G. H. (1894). *The Mission to Uganda,* p. 213.

Porteres, R. (1937). Étude sur les Cafeiers Spontanes de la section 'Des Eucoffeae'. *Ann. Agric. l'Afrique Occidentale,* **1,** 68–91.

Raychaudhuri, S. P. (1941). Studies of Indian red soils. III. General morphological characteristics of some profiles. *Ind. J. Agric. Sci.* **11,** 220–35.

Richards, P. W. (1941). Lowland tropical podsols and their vegetation. *Nature, Lond.,* **148,** 129–31.

Roscoe, J. (1911). *The Baganda.*

Rosevear, R. D. (1942). Soil changes in Enugu plantations. *Farm and Forest,* **3,** 41.

Speke, J. H. (1863). *Journal of the Discovery of the Source of the Nile.*

Spurway, C. H. (1938). Soil testing. *Tech. Bull. Mich. Agric. Exp. Sta.* no. 132.

Stanley, H. M. (1878). *Through the Dark Continent,* p. 198.

Thomas, A S. (1940). Grasses as indicator plants in Uganda. *East Afr. Agric. J.* **6,** 19–22, 77–80.

Thomas, A. S. (1941). The vegetation of the Sese Islands, Uganda. *J. Ecol.* **29,** 330–53.

Thomas, A. S. (1942a). A note on the distribution of *Chlorophora excelsa* in Uganda. *Emp. For. J.* **21,** 1.

Thomas, A. S. (1942b). Lowland tropical podsols in Uganda. *Nature, Lond.,* **149,** 195.

Thomas, A. S. (1944). The vegetation of the Karamoja District, Uganda. *J. Ecol.* **31,** 149–77.

Thomas, A. S. (1945). The vegetation of some hillsides in Uganda. *J. Ecol.* **33,** 10–43.

Vine, H. (1941). A soil catena in the Nigerian cacao belt. *Farm and Forest,* **2,** 137–41.

Wayland, E. J. (1934). Rifts, rivers, rain and early man in Uganda. *J. R. Anthrop. Soc.* **44.**

Worthington, E. B. (1938). *Science in Africa,* p. 16.

THE MORA FORESTS OF TRINIDAD, BRITISH WEST INDIES

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(With six Figures in the Text)

I. DESCRIPTION OF THE FORESTS

Location. The mora forests of Trinidad in the West Indies are tall evergreen forests, in which *Mora excelsa* Benth. is both dominant and gregarious. They are sharply bounded and the mora is not found outside its gregarious assemblages. Mora forest occurs in several different parts of the island, and the blocks of mora forest are of very varying size. The largest area (Fig. 1) is in Mayaro, the south-east corner of Trinidad. Another block, almost as large, covers the foothills in Matura at the eastern end of the Northern Range and there are smaller areas in Cedros, at Paria Bay, behind the Nariva Swamp, in the Aripo valley and at Mount Harris. The size of these forest areas (calculated by planimeter from aerial survey) is approximately as follows: Mayaro, 21,750 ha.; Matura, 13,100 ha.; Cedros, 1440 ha.; Paria, 485 ha.; Nariva, 208 ha.; Mt Harris, 8 ha.; Aripo, 2 ha.; total 36,993 ha. (91,400 acres). This amounts to 17% of the remaining area of natural forest and swamp in the island.

Structure, physiognomy and reproduction. The structure of mora forest is demonstrated diagrammatically in Fig. 2, which is a scale drawing of an actual typical strip of forest 200 ft. (61 m.) long and 25 ft. (7·6 m.) deep measured in the Mayaro district. There is a continuous canopy layer at about 37–43 m. from the ground, the trees being fairly regularly spaced and allowing few or no gaps. Viewed from the air the canopy of mora forest has the same undulating but continuous character as the waves of the sea. Individual crowns are shaped in conformity with the adjacent ones which they touch, fitting together into a most striking mosaic. Mora itself commonly supplies from 85 to 95% of the trees forming the canopy layer, the height of which is most usually about 40 m., though the writer has measured one tree in Cedros of 58 m. (190 ft.). Below the canopy layer two discontinuous tree strata, a middle and a lower story at 12–25 and 3–9 m. respectively, can be vaguely distinguished.

For comparative purposes a similar diagram is given (Fig. 3) of the structure of the 'crappo-guatecare' (*Carapa-Eschweilera*) forests, which are the most widespread type of non-mora moist evergreen forest in Trinidad and adjoin the mora forests in most places. The same three tree stories can be recognized at similar levels, but the uppermost is very discontinuous, consisting of only a few scattered big trees. Canopy is formed by the middle story and the relative numbers in the middle and lower stories are much increased. Viewed from the air these forests appear very irregular, an occasional tall outstanding tree or a patch of such trees amid shorter growth.

Mora forest contains a remarkably large number of big trees. While the average number of individuals per 100 acres (40 ha.) over 1 ft. (30 cm.) girth is about 13,000 compared with 15,000 in the mixed crappo-guatecare (*Carapa-Eschweilera*) forests, the number of trees over 6 ft. (183 cm.) girth is 1725 and over 10 ft. (3·05 m.) girth 450 compared with 500 and 60 respectively.

Lianes are poorly developed in this type of forest; large, thick ropes are rare and crowns relatively little encumbered. Epiphytes are largely confined to the crowns of the big trees and do not often grow lower down. Bromeliads with various aroids, chiefly *Anthurium hookeri* and *Philodendron* spp., are the principal epiphytes. Orchids may be rated as occasional, and epiphytic ferns as rare.

The mora tree is remarkable for the very large size of its plank buttresses, which may spread over 2 m. from the trunk and commonly spring more than 3 m. from the ground. The bark is brownish and scaly, about 5–7 mm. thick, hard and tough. The blaze is pale brown, the sapwood white, the heartwood deep red-brown. The timber is hard, and though resistant to termites it is susceptible to fungus attack and therefore is not durable when in contact with the ground. Mora is evergreen and has pinnate leaves of 6–8 mesophyllous leaflets, which are thin and papery, with a long drip-tip. Flush leaves are pinkish brown in colour. Flushing takes place over the whole tree at once and usually over the whole forest also, at which times the canopy is a striking sight. No observations have been made on the periodicity of flushing.

Shrub, field and ground layers in the forest are composed almost exclusively of young mora seedlings and saplings, which form a dense, scarcely penetrable growth. The small palms *Geonoma vaga*, *Bactris cuesa*, *B. major* and *B. simplicifrons* may become locally frequent; other plants may include *Heliconia* spp., *Ischnosiphon arouma* and *Calathea discolor*, but all are quite subordinate to the young mora.

Mora forest as a whole seeds abundantly every year, though individual trees may not do so. The seed, which falls during the second part of the wet season (November–December), is a heavy bean about 7–10 cm. in length and weighing nearly 0·5 kg. It naturally falls only beneath the parent tree, but the seedling produced is vigorous and able to stand heavy shade, so that the forest floor is densely carpeted with mora seedlings of 1 m. high and upwards. On germination the seedling grows very fast, attaining a height of 80 cm. in a few months, after which growth is slow, the plant just existing in the heavy shade, awaiting the appearance of a gap in the upper canopy. Counts by the writer in the ground layer showed an average per sq. m. of eleven mora seedlings from 80 to 150 cm. in height, two from 1·8 to 3·7 m., and one plant other than a mora.

Floristic composition. In Table 1 is shown a list compiled from 1000 chains (20·1 km.) of belt transect records in the Mayaro district to indicate average stocking per 100 acres (40 ha.) of mora forest. The total number of species in the assemblage is large, eighty-seven different local names having been recorded, some of which cover a group of two or more botanical species, but *Mora excelsa* is dominant to a marked degree, particularly among the larger size classes. Mora, in fact, provides 62·1 % of all trees listed over 1 ft. (30 cm.) girth and 95·5 % of those over 6 ft. (183 cm.). This means that mora is nearly twice as abundant as all the other associated trees put together, and that 95·5 % of all the trees forming the forest canopy are mora.

In a similar list showing the average composition of the predominant type of surrounding non-mora forest, the crappo-guatecare forests (*Carapa-Eschweilera*) (Table 2), it will be seen that the composition is almost exactly the same as that of the mora forest with the single important exception that mora is totally absent. The associated species are relatively more abundant, thus compensating for the absence of mora and bringing the total number of trees per acre to roughly the same figure.

In the north of the island, in Matura, the crappo-guatecare forests contiguous to the

mora are of slightly different composition, belonging to a different faciation. The commonest species are *Aniba panurensis*, *Pachira insignis*, *Sterculia caribaea*, *Chimarrhis cymosa*, *Carapa guianensis*, *Licania biglandulosa*, *Diospyros ierensis* and *Brownea latifolia*. The mora forests of this locality are also of different composition from those of Mayaro. Mora is slightly less abundant, providing 41·5% of the trees over 1 ft. (30 cm.) girth and 86·0% of those over 6 ft. (183 cm.), but the associated species are the same and show the same relative abundance to one another as in the contiguous crappo-guatecare forests of the locality.
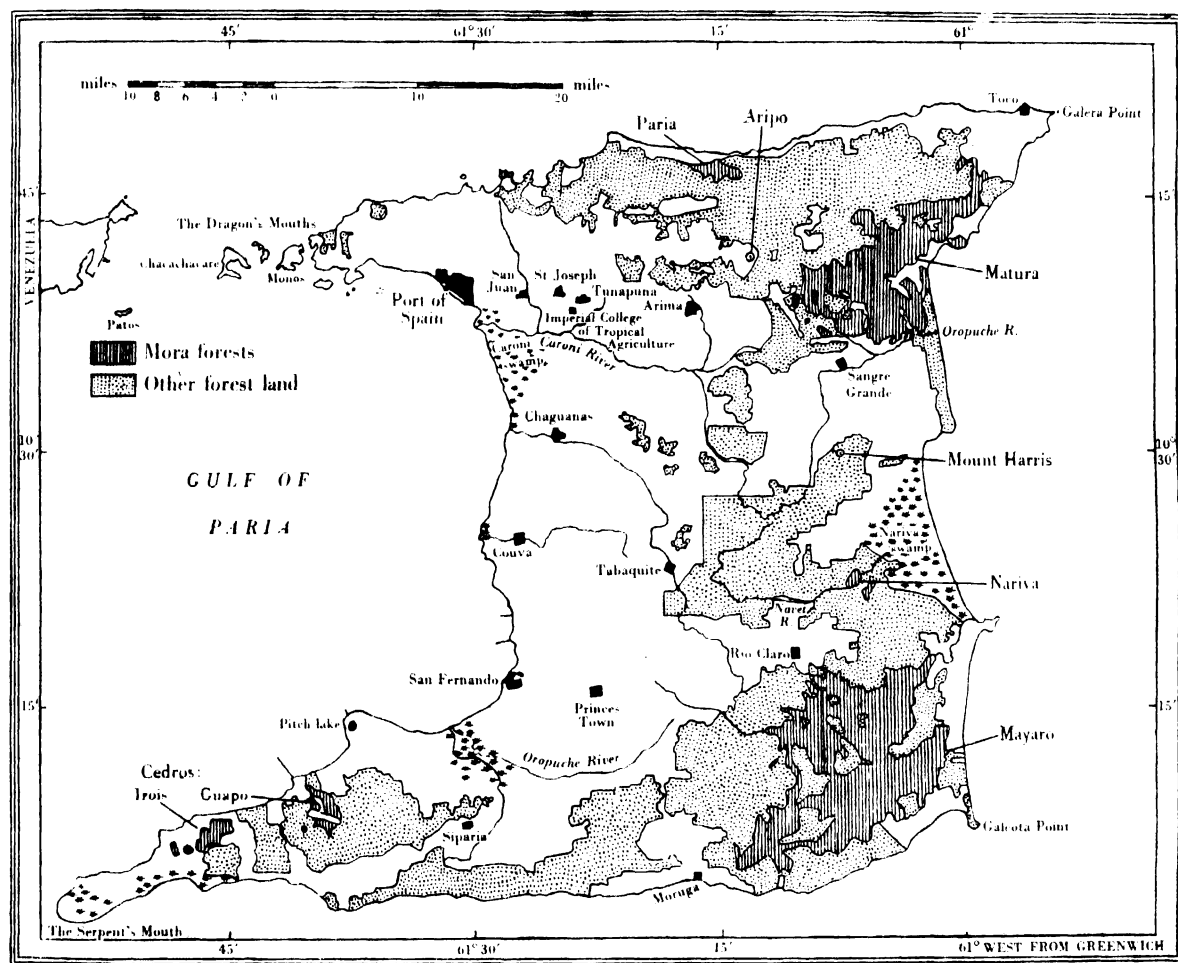
Fig. 1. The distribution of mora and other forest land in Trinidad at the present day.

On the alluvial flats of part of the Matura forest, mora forest adjoins a more specialized type than the common crappo-guatecare, a forest which is strictly a transition or ecotone between the crappo-guatecare and the 'galba-palm' (*Calophyllum*-Palmae) marsh forests of the Long Stretch area farther west. This is a rather lower forest with great abundance of the palms *Jessenia oligocarpa* and *Manicaria saccifera* in the lower levels. Here, too, the composition of the mora forest conforms to that of its neighbour.

Along the south and west boundaries of the Mayaro mora forest drier conditions have produced a slightly more xerophytic forest than the mesic crappo-guatecare which belongs to two different associations, the 'acurel-moussara' (*Trichilia-Brosimum*)—

Fig. 2. Profile diagram of a strip of mora forest, 200 ft. (61 m.) long and 25 ft. (7·6 m.) deep, drawn to scale. Mayaro district, Trinidad.

(See p. 192 for key to index letters on figs. 2 and 3.)

Fig. 3. Profile diagram of a strip of crappo-guatecare (*Carapa-Eschweilera*) forest, 200 ft. (61 m.) long and 25 ft. (7·6 m.) deep. Trinidad.

Table 1. *Estimated average composition per 100 acres (40 ha.). Mora forest in Mayaro*

'P' indicates palm.

	Creole name		Botanical name	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	Over 10	Total
			Species attaining canopy layer											
1.	Mora		*Mora excelsa* Benth.	3413	1147	658	435	400	353	295	263	267	570	7801
2.	Crappo		*Carapa guianensis* Aubl.	477	313	177	129	91	15	9	4	3	1	1219
3.	Olivier mangue		*Terminalia dichotoma* G. F. W. Mey.	50	39	26	34	18	8	4	1	.	.	180
4.	Bloodwood		*Pterocarpus rohrii* Vahl.	17	11	14	10	6	.	4	2	.	1	65
5.	Hogplum		*Spondias mombin* L.	16	14	9	6	4	3	2	2	1	2	59

No. of species 5. No. of individuals 9324

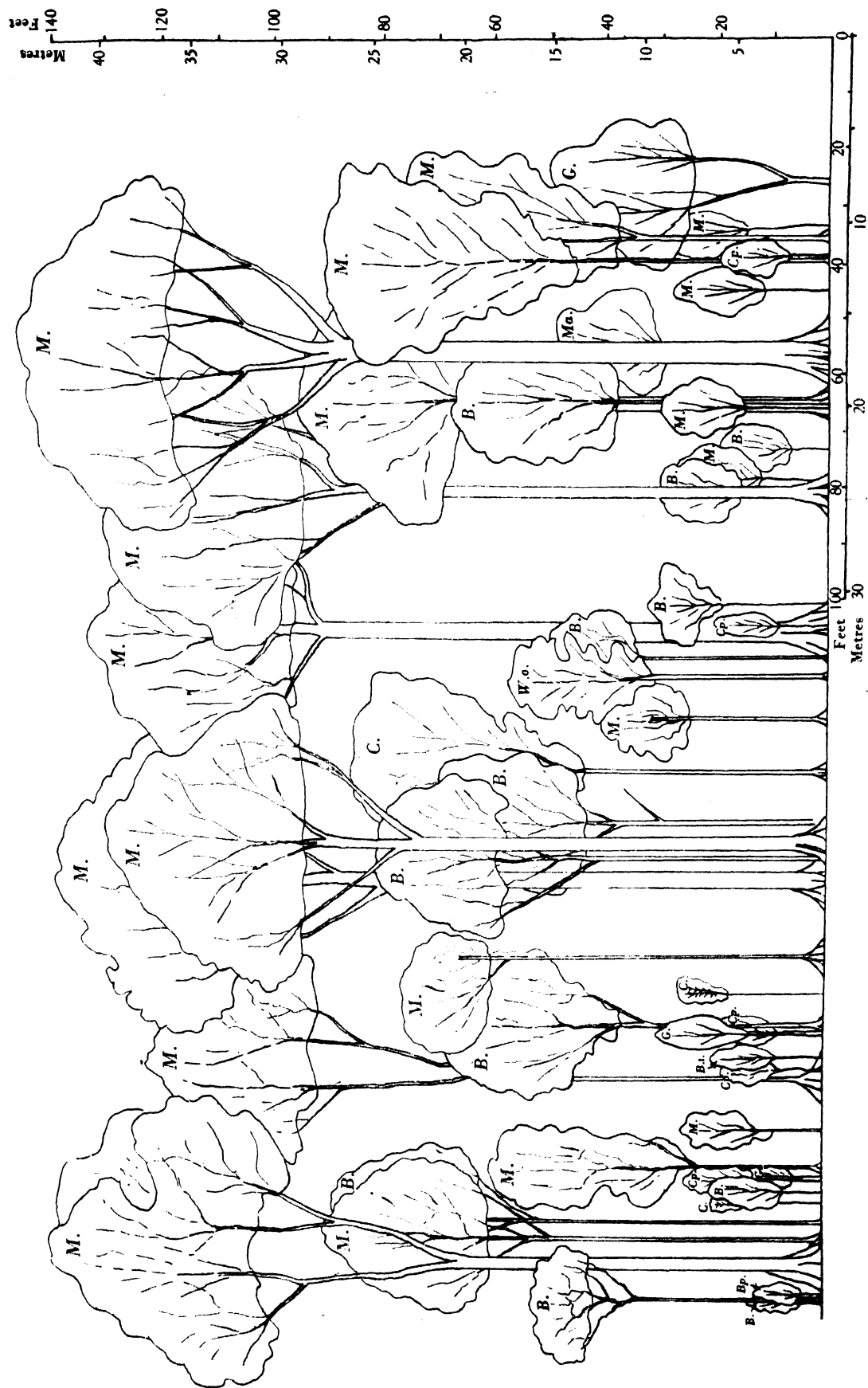|	Creole name		Botanical name	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	Over 10	Total
			Species attaining middle story											
6.	Bois mulatre		*Pentaclethra macroloba* (Willd.) Kuntze	182	159	80	15	.	.	.	.	.	.	436
7.	Wild chataigne		*Pachira insignis* (Sw.) Sav.	88	24	20	1	1	1	.	.	.	.	135
8.	Blackheart		*Clathrotropis brachypetala* (Tul.) Kleinh.	66	30	18	3	3	1	.	.	.	.	121
9.	Mahoe		*Sterculia caribaea* R.Br.	78	34	4	2	.	.	.	.	.	.	118
10.	Guatecare		*Eschweilera subglandulosa* (Steud.) Miers	37	13	8	4	2	2	.	.	.	.	66
11.	Yellow mangue		*Symphonia globulifera* L. fil.	33	14	9	2	1	1	.	.	.	.	60
12.	Toporite		*Hernandia sonora* L.	17	17	16	2	2	2	.	.	.	.	56
13.	Monkeybone		*Mouriri rhizophoraefolia* DC.	12	12	12	4	2	.	.	.	.	.	42
14.	Redwood		*Guarea guara* (Jacq.) P. Wilson	12	8	5	8	.	.	.	.	.	.	33
15.	Laurier canelle		{ *Aniba panurensis* Mez. and	6	6	14	1	2	1	.	.	.	.	30
16.			{ *A. trinitatis* (Meissn.) Mez.											
17.	Pois doux		*Inga* spp.	14	6	2	6	.	.	.	.	.	.	28
18.	Balata		*Manilkara bidentata* (A.DC.) Chev.	10	4	7	2	1	1	.	.	.	.	25
19.	Malbalata		*Pouteria minutiflora* (Britton) Sandwith	10	1	6	4	3	.	.	.	.	.	24
20.	Bois charbon		*Diospyros ierensis* Britton	16	2	2	1	2	.	.	.	.	.	23
21.	Cajuca		*Virola surinamensis* (Rol.) Warb.	6	8	4	2	1	.	.	.	.	.	21
22.	Angelin		*Andira inermis* (Wright) H.B.K.	8	3	5	3	.	.	.	.	.	.	19
23.	Bois l'orme		*Guazuma ulmifolia* Lam.	5	2	.	2	1	1	.	.	.	.	11
24.	Waterlocust		*Crudia glaberrima* (Steud.) Macbride	4	2	.	2	1	1	.	.	.	.	10
25.	Olivier		{ *Terminalia amazonia* (J. F. Gmel.) Exell.	2	1	2	1	.	2	.	.	.	.	8
26.			{ *Buchenavia capitata* (Vahl.) Eichl.											
27.	Laurier mattack		*Nectandra surinamensis* Mez.	2	1	1	1	1	.	.	.	.	.	6
28.	Puni		*Pithecellobium jupunba* (Willd.) Urb.	2	1	.	1	.	1	.	.	.	.	5
29.	Goodbread		*Pisonia salicifolia* Heimerl.	1	1	.	.	2	.	.	.	.	.	4
30.	Poui		*Tabebuia rufescens* J. R. Johnst.	.	2	.	.	2	.	.	.	.	.	4
31.	Conoré		*Lonchocarpus sericeus* (Poir.) H.B.K.	.	1	.	.	1	1	.	.	.	.	3
32.	Bosoo		*Fagara trinitensis* (Williams) J. S. Beard	.	.	2	1	.	.	.	.	.	.	3
33.	Tapana		*Hieronyma caribaea* Urb.	1	.	.	1	.	.	.	.	.	.	2
34.	Cannonball		*Couroupita guianensis* Aubl.	.	.	.	2	.	.	.	.	.	.	2
35.	Milkwood		*Sapium aucuparium* Jacq.	1	1	.	.	.	.	.	.	.	.	2
36.	'Arena' sardine		*Pera arborea* Mutis.	1	.	.	1	.	.	.	.	.	.	2
37.	Figuier		*Ficus tobagensis* Urb.	.	.	.	.	2	.	.	.	.	.	2
38.	Galba		*Calophyllum lucidum* Benth.	.	1	.	.	.	.	.	.	.	.	1
39.	Silk cotton		*Ceiba occidentalis* (Spreng.) Burkill	.	.	.	1	.	.	.	.	.	.	1
40.	Black fiddlewood		*Vitex divaricata* Sw.	.	.	1	.	.	.	.	.	.	.	1
41.	Acoma		*Sideroxylon quadriloculare* Pierre	.	.	.	1	.	.	.	.	.	.	1
42.	Sandbox		*Hura crepitans* L.	.	.	.	.	1	.	.	.	.	.	1
43.	Roble		*Platymiscium trinitatis* Benth.	.	.	1	.	.	.	.	.	.	.	1
44.	Bois lissette		*Mouriri marshallii* Burtt Davy & Sandwith	.	.	1	.	.	.	.	.	.	.	1

No. of species 39. No. of individuals 1308

	Creole name		Botanical name	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	Over 10	Total
			Species confined to lower story											
45.	Bois pois		*Swartzia pinnata* Willd.	401	61	.	.	.	.	.	.	.	.	462
46.	Cooperhoop		*Brownea latifolia* Jacq.	413	.	.	.	.	.	.	.	.	.	413
47.	Carat	P	*Sabal* sp.	.	330	.	.	.	.	.	.	.	.	330
48.	Manac	P	*Euterpe langloisii* Burret	228	.	.	.	.	.	.	.	.	.	228
49.	Cocorite	P	*Maximiliana elegans* Karst.	.	73	.	.	.	.	.	.	.	.	73
50.	Bois tatou		*Rudgea freemani* Sprague & Williams	68	4	.	.	.	.	.	.	.	.	72
51.	Cocochat		*Hirtella racemosa* Lam.	31	6	1	.	.	.	.	.	.	.	38
52.	Keskidee		*Vismia* spp.	30	.	.	.	.	.	.	.	.	.	30
53.	Acurel		*Trichilia smithii* C.DC.	18	6	.	.	.	.	.	.	.	.	24
54.	Gatia		*Brosimum aubletii* Poepp. & Endl.	20	4	.	.	.	.	.	.	.	.	24
55.	Soiebo		*Rheedia* sp.	23	.	.	.	.	.	.	.	.	.	23
56.	Mahoe piment		*Daphnopsis caribaea* Gr.	14	7	.	.	.	.	.	.	.	.	21
57.	Bois canon		*Cecropia peltata* L.	11	6	1	.	.	.	.	.	.	.	18
58.	Wakamy		*Warszewiczia coccinea* (Vahl.) Kl.	16	.	.	.	.	.	.	.	.	.	16
59.	Fruta paloma		*Hirtella triandra* Sw.	5	5	5	.	.	.	.	.	.	.	15
60.	Wild kaimit		*Chrysophyllum argenteum* Jacq.	6	6	2	.	.	.	.	.	.	.	14
61.	Wild guava		*Myrtaceae* spp.	13	.	.	.	.	.	.	.	.	.	13
62.	Pipewood		*Casearia* sp.	13	.	.	.	.	.	.	.	.	.	13
63.	Cuchape		*Coccoloba latifolia* Lam.	12	.	.	.	.	.	.	.	.	.	12
64.	Wild coffee		*Rubiaceae* spp.	8	2	.	.	.	.	.	.	.	.	10
65.	Black grape		*Coccoloba fallax* Lindau.	10	.	.	.	.	.	.	.	.	.	10
66.	Wild cashima		{ *Rollinia mucosa* (Jacq.) Baill.	8	1	.	.	.	.	.	.	.	.	9
67.			{ *R. exsucca* (Dun.) A.DC.											

Table 1 (continued)

Creole name	Botanical name	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	Over 10	Total
68. Wild orange	*Swartzia simplex* (Sw.) Spreng.	7	.	.	.	.	.	.	.	.	.	7
69. Niauré	*Calliandra guildingii* Benth.	5	.	.	.	.	.	.	.	.	.	5
70. Carimbo	*Guarea glabra* Vahl.	5	.	.	.	.	.	.	.	.	.	5
71. Wild cocoa	*Tovomita eggersii* Vesque	3	.	1	.	.	.	.	.	.	.	4
72. Laylay	*Cordia* spp.	1	.	2	.	.	.	.	.	.	.	3
73. Sardine	*Miconia* spp.	3	.	.	.	.	.	.	.	.	.	3
74. White grape	*Coccoloba venosa* L.	3	.	.	.	.	.	.	.	.	.	3
75. Bois flot	*Ochroma pyramidale* (Cav.) Urb.	1	1	1	.	.	.	.	.	.	.	3
76. Bois toucan	*Laetia procera* (Poepp. & Endl.) Eichl.	.	.	3	.	.	.	.	.	.	.	3
77. Juniper	*Genipa americana* L.	2	.	.	.	.	.	.	.	.	.	2
78. Laurier cypre	*Ocotea oblonga* (Meissn.) Mez.	2	.	.	.	.	.	.	•	.	.	2
79. Maraquil	*Cupania americana* L.	1	1	.	.	.	.	.	.	.	.	2
80. Ironwood	*Isertia parviflora* Vahl.	2	.	.	.	.	.	.	.	.	.	2
81. White savonette	*Lonchocarpus punctatus* H.B.K.	2	.	.	.	.	.	.	.	.	.	2
82. Wild imortelle	*Erythrina pallida* Br. & Rose	1	.	.	.	.	.	.	.	.	.	1
83. Palmiste P	*Roystonea oleracea* Cook	.	.	.	1	.	.	.	.	.	.	1
84. Obi	*Trichilia trinitensis* Juss.	1	.	.	.	.	.	.	.	.	.	1
85. Beefwood	*Pisonia* sp.	.	1	.	.	.	.	.	.	.	.	1
86. Courapara	?	.	.	1	.	.	.	.	.	.	.	1
87. Debasse	*Eugenia* sp.	1	.	.	.	.	.	.	.	.	.	1

No. of species 43.   No. of individuals 1920

Total no. of species 87. Total no. of individuals 12,552 or 126 per acre (0·405 ha.).

Table 2. *Estimated average composition per 100 acres (40 ha.).*
'Crappo-Guatecare' forest (Carapa-Eschweilera)

Creole name	Botanical name	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	Over 10	Total
Species becoming emergent trees												
1. Crappo	*Carapa guianensis* Aubl.	358	220	171	206	102	36	27	2	3	4	1129
2. Wild chataigne	*Pachira insignis* (Sw.) Sav.	204	135	84	79	60	19	14	5	3	.	603
3. Guatecare	*Eschweilera subglandulosa* (Steud.) Miers	108	69	35	30	20	2	6	1	1	1	273
4. Waterlocust	*Crudia glaberrima* (Steud.) Macbride	157	57	29	15	4	3	3	.	.	1	269
5. Mahoe	*Sterculia caribaea* R.Br.	98	32	24	35	8	.	2	1	.	.	200
6. Yellow mangue	*Symphonia globulifera* L. fil.	44	28	36	20	6	2	.	.	.	.	136
7. Hogplum	*Spondias mombin* L.	26	13	28	14	15	14	9	4	3	10	136
8. Pois doux	*Inga* spp.	58	28	8	16	6	5	.	.	.	.	121
9. Bloodwood	*Pterocarpus rohrii* Vahl.	36	18	24	18	6	4	1	5	5	2	119
10. Jiggerwood	*Bravaisia integerrima* (Spreng.) Standl.	36	32	28	6	3	2	3	2	.	.	112
11. Cajuca	*Virola surinamensis* (Rol.) Warb.	40	26	16	4	8	1	3	2	3	5	108
12. Sackysac	*Inga* spp.	30	20	18	17	6	5	.	.	.	.	96
13. Toporite	*Hernandia sonora* L.	16	10	20	20	6	4	4	2	.	.	82
14. Balata	*Manilkara bidentata* (A.DC.) Chev.	5	6	7	6	9	5	4	3	2	3	50
15. Purpleheart	*Peltogyne porphyrocardia* Gr.	18	6	4	2	2	2	.	1	1	2	38
16. Conoré	*Lonchocarpus sericeus* (Poir.) H.B.K.	9	6	6	5	3	2	.	1	.	1	33
17. White olivier	*Terminalia amazonia* (J. F. Gmel.) Exell.	3	4	3	6	3	4	2	2	2	3	32
18. Angelin	*Andira inermis* (Wright) H.B.K.	8	5	4	2	1	1	2	.	1	.	24
19. Olivier mangue	*Terminalia dichotoma* G. F. W. Mey.	6	6	4	1	2	.	1	1	1	.	22
20. Tapana	*Hieronyma caribaea* Urb.	2	1	4	2	4	2	2	2	.	.	19
21. Black fiddlewood	*Vitex divaricata* Sw.	4	3	2	.	1	1	1	1	.	.	16
22. Cedar	*Cedrela mexicana* Roem.	1	1	.	2	3	1	2	1	1	2	14
23. Roble	*Platymiscium trinitatis* Benth.	3	4	.	2	1	2	.	1	1	.	14
24. Silk cotton	*Ceiba occidentalis* (Spreng.) Burkill	1	2	2	2	1	2	1	1	1	.	13
25. Sandbox	*Hura crepitans* L.	1	1	3	.	1	1	.	1	1	2	11
26. Figuier	*Ficus tobagensis* Urb.	1	1	2	.	1	1	1	.	.	3	10
27. Locust	*Hymenaea courbaril* L.	.	1	.	1	.	2	.	.	1	.	5
28. Cannonball	*Couroupita guianensis* Aubl.	1	.	1	.	.	.	.	.	.	2	4
29. Acoma	*Sideroxylon quadriloculare* Pierre	.	.	.	1	.	1	.	.	.	1	3
30. Yellow olivier	*Buchenavia capitata* (Vahl.) Eichl.	.	1	.	.	1	.	1	.	.	.	3
31. Balsam	*Copaifera officinalis* L.	.	.	.	.	1	.	.	.	.	.	1
Species attaining canopy layer												
32. Bois mulatre	*Pentaclethra macroloba* (Willd.) Kuntze	860	716	364	209	88	12	.	.	.	.	2249
33. Acurel	*Trichilia smithii* C.DC.	134	200	80	25	15	.	.	.	.	.	454
34. Redwood	*Guarea quara* (Jacq.) P. Wilson	198	81	45	12	.	.	.	.	.	.	336
35. Monkeybone	*Mouriri rhizophoraefolia* DC.	93	84	84	43	9	.	.	.	.	.	313
36. Bois charbon	*Diospyros ierensis* Britton	67	59	29	25	.	.	.	.	.	.	180
37. Blackheart	*Clathrotropis brachypetala* (Tul.) Kleinh.	51	48	32	10	4	1	.	.	.	.	146
38. 39. Laurier canelle	{ *Aniba panurensis* Mez. and *A. trinitatis* (Meissn.) Mez.	43	36	19	12	7	.	.	.	.	.	117
40. Bois canon	*Cecropia peltata* L.	66	23	20	3	.	.	.	.	.	.	112

No. of species 31.   Total no. of individuals 3696

Table 2 (continued)

Creole name	Botanical name	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	Over 10	Total
41. Wild guava	Myrtaceae spp.	34	32	26	6	.	.	.	.	.	.	98
42. Malbalata	Pouteria minutiflora (Britton) Sandwith	33	28	15	10	4	1	.	.	.	.	91
43. Fruta paloma	Hirtella triandra Sw.	26	32	12	3	.	.	.	.	.	.	73
44. Gommier	Protium insigne Engl.	22	18	10	8	.	.	.	.	.	.	58
45. Wild coffee	Eugenia confusa DC.	26	16	8	6	1	.	.	.	.	.	57
46. Laylay	Cordia spp.	30	1	1	1	.	.	.	.	.	.	33
47. Palmiste P	Roystonea oleracea Cook.	.	30	.	.	.	.	.	.	.	.	30
48. Juniper	Genipa americana L.	20	5	4	1	.	.	.	.	.	.	30
49. Sardine	Miconia spp.	12	8	8	1	.	.	.	.	.	.	29
50. Courapara	?	6	2	6	6	4	.	.	.	.	.	24
51. Moussara	Brosimum alicastrum Sw.	6	5	3	4	2	1	.	.	.	.	21
52. Bosoo	Fagara trinitensis (Williams) J. S. Beard	5	4	5	4	2	.	.	.	.	.	20
53. Keskidee	Vismia spp.	11	4	3	2	.	.	.	.	.	.	20
54. Wild cashima	Rollinia mucosa (Jacq.) Baill.	8	4	3	4	.	.	.	.	.	.	19
55. Bois toucan	Laetia procera (Poepp. & Endl.) Eichl.	5	4	4	4	1	.	.	.	.	.	18
56. Wakamy	Warszewiczia coccinea (Vahl.) Kl.	9	4	3	1	.	.	.	.	.	.	17
57. White fiddlewood	Vitex capitata Vahl.	4	2	4	2	2	1	1	.	.	.	16
58. Bois l'orme	Guazuma ulmifolia Lam.	4	4	4	4	.	.	.	.	.	.	16
59. Wild calabash	Tabebuia stenocalyx Sprague & Williams	5	3	3	2	2	.	.	.	.	.	15
60. Goodbread	Pisonia cuspidata Heimerl.	5	2	2	1	.	.	.	.	.	.	10
61. Poui	Tabebuia rufescens J. R. Johnst.	5	3	2	2	1	.	.	.	.	.	13
62. L'epinet	Fagara martinicensis Lam.	5	4	2	2	.	.	.	.	.	.	13
63. Mahoe piment	Daphnopsis caribaea Gr.	4	4	4	.	.	.	.	.	.	.	12
64. Milkwood	Sapium aucuparium Jacq.	3	3	2	2	1	1	.	.	.	.	12
65. Puni	Pithecellobium jupunba (Willd.) Urb.	2	2	2	1	1	1	.	.	.	.	9
66. Saltfishwood	Machaerium robinifolium (DC.) Vogel.	3	1	2	2	1	.	.	.	.	.	9
67. Serrette	Byrsonima spicata (Cav.) Rich.	2	1	2	1	2	.	.	.	.	.	8
68. Acoma piquant	Bumelia grisebachii Pierre	2	2	2	1	1	.	.	.	.	.	8
69. Bois flot	Ochroma pyramidale (Cav.) Urb.	2	2	1	1	.	1	.	.	.	.	7
70. Laurier mattack	Nectandra martinicensis (Jacq.) Mez.	1	1	2	.	.	1	.	.	.	.	5
71. Maraquil	Cupania americana L.	2	1	1	.	.	.	.	.	.	.	4
72. Bois lissette	Mouriri marshallii Burtt Davy & Sandwith	2	.	1	.	1	.	.	.	.	.	4
73. Incense	Protium guianense (Aubl.) March.	2	.	1	.	.	.	.	.	.	.	3
74. Laurier cypre	Ocotea oblonga (Meissn.) Mez.	1	1	1	.	.	.	.	.	.	.	3
75. Laurier 'zaboca	Ocotea glomerata (Nees) Mez.	1	.	1	.	.	.	.	.	.	.	2
76. Jereton	Didymopanax morototoni (Aubl.) Dcne. & Planch.	.	1	.	1	.	.	.	.	.	.	2

No. of species 45   No. of individuals 4716

Species confined to lower story

Creole name	Botanical name	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	Over 10	Total
77. Carat P	Sabal sp.	.	1493	.	.	.	.	.	.	.	.	1493
78. Cooperhoop	Brownea latifolia Jacq.	396	256	128	4	.	.	.	.	.	.	784
79. Bois pois	Swartzia pinnata Willd.	166	106	90	3	.	.	.	.	.	.	365
80. Manac P	Euterpe langloisii Burr.	312	.	.	.	.	.	.	.	.	.	312
81. White grape	Coccoloba venosa L.	204	83	.	.	.	.	.	.	.	.	287
82. Black grape	Coccoloba fallax Lindau.	187	96	.	.	.	.	.	.	.	.	283
83. Cuchape	Coccoloba latifolia Lam.	108	82	4	.	.	.	.	.	.	.	194
84. Carimbo	Guarea glabra Vahl.	94	58	8	.	.	.	.	.	.	.	160
85. Bois taton	Rudgea freemani Sprague & Williams	74	34	3	.	.	.	.	.	.	.	111
86. Debasse	Myrtaceae spp.	108	.	.	.	.	.	.	.	.	.	108
87. Cocorite P	Maximiliana elegans Karst.	.	105	.	.	.	.	.	.	.	.	105
88. Soiebo	Rheedia sp.	54	20	3	.	.	.	.	.	.	.	77
89. Pipewood	Casearia decandra Jacq.	60	10	.	.	.	.	.	.	.	.	70
90. Palma real P	Jessenia oligocarpa Griseb. & Wendl.	.	64	.	.	.	.	.	.	.	.	64
91. Wild orange	Swartzia simplex (Sw.) Spreng.	30	20	6	.	.	.	.	.	.	.	56
92. Wild kainit	Chrysophyllum argenteum Jacq.	15	15	8	2	.	.	.	.	.	.	40
93. Cocochat	Hirtella racemosa Lam.	20	15	.	.	.	.	.	.	.	.	35
94. Gatia	Brosimum aubletii Poepp. & Endl.	11	10	.	.	.	.	.	.	.	.	21
95. Wild immortelle	Erythrina pallida Br. & Rose	15	.	.	.	.	.	.	.	.	.	15
96. Wild sapodilla	Morisonia americana L.	5	4	.	.	.	.	.	.	.	.	9
97. Wild tamarind	Basanacantha phyllosepala Spr. & Williams	8	.	.	.	.	.	.	.	.	.	8
98. Cutlet	Citharexylum fruticosum L. var. Brittonii Moldenke	4	2	2	.	.	.	.	.	.	.	8
99. Marc	Talisia hexaphylla Vahl.	7	.	.	.	.	.	.	.	.	.	7
100. Lardwood	Aegiphila integrifolia (Jacq.) Jacks	4	2	.	.	.	.	.	.	.	.	6
101. Butterwood	Maba inconstans Griseb.	3	2	.	.	.	.	.	.	.	.	5
102. Bois la glie	Ryania speciosa Vahl.	4	1	.	.	.	.	.	.	.	.	5
103. Beefwood	Pisonia sp.	3	.	.	.	.	.	.	.	.	.	3
104. Gasparee	Esenbeckia spp.	2	.	.	.	.	.	.	.	.	.	2

No. of species 28.   Total no. of individuals 4633

Total no. of species 104. Total no. of individuals 13,045 or 130 per acre.

'gommier' (*Protium insigne*) faciation—and the 'purple heart' (*Peltogyne*). The former is characteristic of sandy soils and the latter of red clays. The contiguous mora shows the usual conforming modifications and on some red clay ridges there is a mixed 'mora-purpleheart' forest.

The boundary of a mora forest is usually sharp; it shows up plainly in aerial photographs and will seldom be found to correspond to any physical feature or any natural boundary to be seen in the field. Sometimes young sapling growth of mora continues for a short distance beyond the last large trees. In the Guapo district, however, scattered mora trees and small patches of mora are to be found strung out along stream banks above the main block of mora forest, and in the Ortoire Basin (part of the Mayaro district) Gunther (1942) has recognized two types intermediate between mora forest proper and crappo-guatecare, which he calls 'Mora Mixed' and 'Mixed Forest with Mora'. He does not show their distribution to be at all wide. Apart from this, isolated mora trees can never be found in non-mora forests as they are in Guiana (Davis & Richards, 1933–4).

Habitat. The mora forests of Trinidad are found only in the lowlands and generally in their lower-lying parts. Mora forests in the north cover part of the valleys and foothills of the Northern Range, but are not found above an altitude where the crappo-guatecare forests of the lowlands would normally give way to mountain rain forests, nor are they found on any really steep slopes. The Paria and Aripo mora forests are confined to valley bottoms and lower slopes and the Matura forest reaches its limit at the foot of the main Oropouche ridge. The maximum altitude at which mora forest occurs is about 180 m. above sea-level. The great part of the Matura forest and of the other mora forests is situated at elevations below 60 m. and is sometimes undulating, sometimes flat and swampy. The southern part of the Matura forest stands on a series of alluvial terraces of various ages from Pleistocene to Recent. Drainage—both lateral and of the subsoil— is throughout very bad, and in places the mora occupies deep swamps, filled with water throughout the year. Part of the Mayaro forest covers the Ortoire, Moruga and other river basins and is low-lying and swampy. Part, on the other hand, covers a sharply undulating country of steep little ridges and deep ravines. In Cedros the Guapo and Cap de Ville areas are low-lying and follow rivers, but the Irois area is almost all undulating.

There is thus no justification for correlating the presence or absence of mora with topography.

The mora forests are found in the wetter parts of Trinidad generally where the rainfall exceeds 200 cm. per annum, though in some parts they receive as little as 150 cm. The year is divided into a dry and a rainy season, January–May and June–December respectively. The dry season is never absolutely rainless, and there are frequently at least 5 cm. of rain a month while it is in progress. There is usually a slight break (*petite carême*) in the rainy season about September–October, dividing it into two parts. Temperatures are tropical and somewhat equable. A comparison of the rainfall map (Fig. 4) with Fig. 1 shows that the distribution of mora is not directly related to precipitation.

The soils beneath mora forests are very diverse, and most of the soil types of the island are represented. All are derived from sedimentary deposits, mainly sands, silts and clays. The resulting soils are brown or red in colour and may be either deep or shallow, friable or compact, freely draining or with impeded subsoil drainage. They are generally of low fertility, and no calcareous soils occur in or near the mora forests. In the low-lying, flat areas which comprise perhaps half of the total area of mora forest there are high water-tables which are presumably subject to seasonal fluctuation. Undulating lands are well drained, and there is not generally any water table in the accepted sense. There are thus no particular soil types characteristic of mora forest.

The greater part of the mora forests have been but little disturbed. Certain restricted areas have been cleared for agriculture and others have suffered from fire, but mora, except in war time, has not commanded a large market and the forests appear to be mainly in a virgin condition.

Over 100 in. (254 cm.)   80–100 in. (203 354 cm.)   65–80 in. (165–203 cm.)

55–65 in. (140–165 cm.)   Under 50 in. (140 cm.)
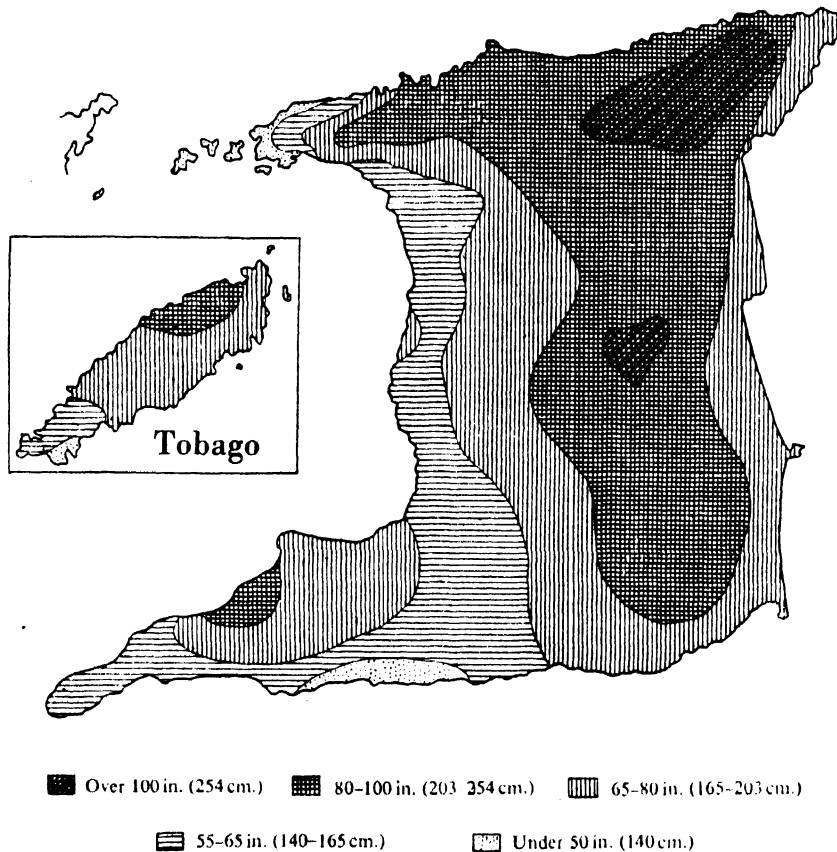
Fig. 4. Rainfall map of Trinidad (after Marshall).

II. Ecological Relationships

The problem. The distribution of mora forests of Trinidad does not appear to be limited by any discoverable environmental conditions or set of conditions. In the absence of any precise cause, it is puzzling to find that in certain restricted areas the mixed association of forest trees is replaced by a single species, which is so markedly gregarious that within the areas where it occurs it is twice as abundant as all the other associated species put together.

Marshall's conclusions. Marshall (1934) discussed the mora problem in detail and arrived at the conclusion that the species is invasive. He cited as evidence the dense growth of young saplings along the edge of mora forests, giving the impression of an onward march, the power of the tree to bear shade and the copious production of seed. He showed also that the species associated with mora represent the type of forest which, as far as can be judged, would occur in the area were mora not present. Marshall regarded all cases where mora appeared to be related to soil or other natural conditions

· as purely fortuitous. Marshall afterwards restated his views (1939), adding the qualification that the tree is 'decidedly hygrophilous' [*sic*] and that it might be expected to invade readily where soil moisture is abundant and perhaps be unable to colonize a 'soil poor in water-holding qualities'.

It seems unlikely that this view can be seriously challenged. It seems indisputable that mora is invading the crappo-guatecare forests, and that if undisturbed by man it would eventually come to dominate them over the whole island. We should not expect it to invade, except perhaps as a casual intruder, the Montane Forests, the Semi-evergreen
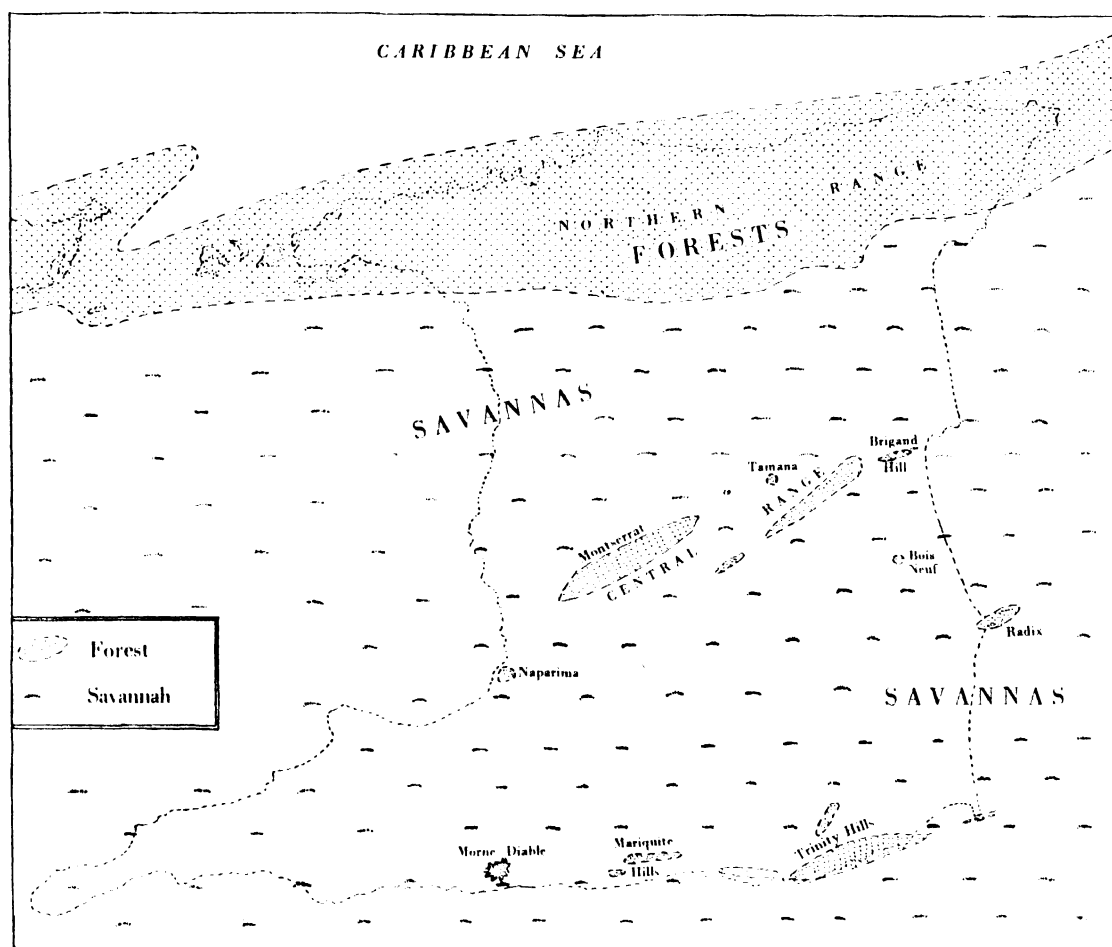
Fig. 5. The probable vegetation of the Trinidad region at the close of the Pleistocene. Gallery forests have been omitted.

and Deciduous Seasonal Forests, herbaceous swamps and savannas. Two secondary problems, however, remain unanswered. Why is mora gregarious? Why is invasion taking place only at the present day?

Gunther's conclusions. Gunther (1942) criticized certain of Marshall's views. His paper was originally written before the appearance of Marshall's second work in 1939, and by the date of publication Marshall had already met the objections. Gunther found that in the Ortoire Basin mora became highly gregarious on flat and swampy areas, and that on sloping or hilly land it was not so clearly dominant or was even absent altogether. Gunther admitted his adherence to the invasion theory, but held that mora would only

St Joseph

Ferry

Pierreville
Plaisance

St Margaret

Galeota Pt
Pt Blanquaires

MAYARO BAY

Bande-de-l'Est

Guayaguayare
White Ids.
GUAYAGUAYARE
BAY

Gran Cayo Pt

Pt Casse Cou

Pt Citron

Pta. Tablas

C. Casa Cruz

Canari Pt

Alcatraz Pt
Canari Bay

Moruga Pt

Miram

Moruga

CAT'S HILL
RESERVE

MORUGA RESERVE

TRINITY HILLS
RESERVE

ORTOIRE WINDBELT RESERVE

RIO RESERVE

Ortoire River

Poole River

Mora burnt in
1920

Ecclesville

Libertville   RIO CLARO

Poole Sta.

Poole
Fonrose

Tableland

Mora forests

Crappo-guatecare forests

Acurel-moussara and
purpleheart forests

0 1 2 3 4 5 miles

invade to the maximum extent on swampy sites and that on rising ground its progress would be limited.

Marshall's modification of his earlier standpoint in the matter of water relations seems more acceptable than Gunther's view. Gunther, unfortunately, was dealing only with a very limited section of one of the mora forests, a section lying, moreover, on the very fringe of the main mora forest. At such a point, therefore, one might expect to find varying degrees of colonization, highly gregarious mora on sites most favourable to it, mixed mora on less favourable sites, since mora would probably invade the former more rapidly. This does not mean that the less favourable sites would not in time become completely colonized. Study of other mora forests, some of which are in mountainous country, proves this point. In fact, areas of mixed mora such as are described by Gunther are rare and occur only near the fringes of mora forests. Naturally mora has not a universal range. Certain sites will be hostile to it, but it would appear that these are not as numerous and widespread as Gunther holds.

The mora forests of British Guiana. In the British and Venezuelan Guianas there are forests of *Mora excelsa* similar to those found in Trinidad. These have been studied by Davis (1929) in the North-West District of British Guiana and in the neighbourhood of Moraballi Creek on the Essequibo by Davis & Richards (1933–4). Contrary to conditions in Trinidad, in the Guianas mora may be found as an occasional single individual in many types of forest. In the localities of British Guiana that have received study, it becomes gregarious and forms definite mora forest chiefly on low-lying and swampy riverain flats with high water table. Even here it does not appear to be so markedly gregarious as in Trinidad, for at Moraballi Creek, Davis & Richards (1933–4) found that *M. excelsa* composed 23·4 % of the trees over 1 ft. (30 cm.) girth in mora forest. These authors were of the opinion that the optimum conditions for the species are not those under which it becomes dominant. The forests of the coast and near interior of Guiana are tall rain forests where the struggle for existence is, presumably, severe. Competition may be so intense on sites which are the optimum for mora as to relegate it to the status of occasional. Mora, however, evidently will tolerate a very wide range of conditions, and on swampy sites with high water table, which would be adverse to most other species, it thrives sufficiently well to assume dominance and to form a gregarious mora forest. Davis & Richards found the same dense growth of young mora seedlings and saplings covering the ground in mora forest as in Trinidad, but where a single individual occurred in another type of forest, such young seedling growth was to be observed only immediately beneath the parent. It would appear that young mora has considerable power of bearing the shade of its own species, but that a similar power does not exist with regard to the shade of other trees.

The seed of mora is so large that it is not readily dispersed, and the fact that the tree is occasional throughout the rain forests of Guiana indicates that it has attained full distribution there. No question can arise that gregarious mora may be advancing into other forests. Davis & Richards found five forest types (of which *M. excelsa* forest was one) at Moraballi Creek, each related to a definite habitat and in apparent equilibrium one with another. Mora forest here and according to Davis in the North-West District was definitely characteristic of swampy riverain flats. In the further interior of British Guiana, the writer was informed in conversation by the Conservator of Forests, Mr B. R. Wood, there are places where mora forest is no longer restricted to riverain flats,

but occurs on hilly ground. It appears probable that the non-mora forests in this region are no longer properly rain forests, but are Evergreen Seasonal Forests (Beard, 1944) like the crappo-guatecare type of Trinidad and are, therefore, of more open structure than rain forests.

Vegetation cycles in Trinidad. Studies of the fossil flora of Trinidad have been made by Hollick (1924) and Berry (1925). The fifty-five species of plants discovered, mainly in Miocene beds, indicate moist evergreen forests but little different from those of the present day. No species of *Mora* is represented in these deposits, but the forests from which the material was derived were apparently either rain forests or Evergeen Seasonal Forests similar to the modern crappo-guatecare.

The existence of such forests fourteen million years ago does not legitimately imply that there has been a continuous forest cover on Trinidad ever since. There have been geological cycles with accompanying vegetational cycles. The particular borderland of South America where Trinidad stands has been in continual oscillation since the Mesozoic, open-sea phases alternating with lagoon and land phases. The vegetation of the area will have varied greatly according as conditions were those of a deltaic region, a young or an old alluvial plain or of a dissected and undulating topography. On emergence of land from the water, succession begins with mangrove and herbaceous swamp vegetation, and on further uplift and the drying of the land the young alluvial soils become covered with moist evergreen forest (assuming a constant climate). Later, as the soils age and become compacted and ill-drained, the forests retreat to the *vegas* of the rivers and become 'gallery forests' in vast stretches of savanna. If the savanna-covered peneplain is dissected and converted into an undulating region the forests will return.

During Pleistocene times the area that is now Trinidad was a part of continental South America and consisted for the most part of a vast, level plain which was co-extensive with the great *llanos* of the Orinoco. By reason of the absence either of further aggradation or erosion, the soils of these ill-drained level flats developed characteristic impeded horizons and the vegetation became a savanna, such as still covers the Venezuelan *llanos*. All Trinidad must have been savanna-clad at that time, save for the Northern and Central Ranges and isolated hills in the south, and the river *vegas* where 'gallery forests' meandered, trees having persisted here due to the continuance of favourable drainage conditions. The map in Fig. 5 gives a conjectural picture of conditions at that time. A great Proto-Orinoco river must have entered the sea far to the east of its present mouths and taken a course parallel to the south coast of Trinidad.

Earth movements in subrecent times have uplifted Trinidad slightly and depressed the areas off its east, west and south coasts, causing the formation of the Gulf of Paria — detaching Trinidad from the mainland—and the retreat of the Proto-Orinoco mouths to their present position. Consequently, the former peneplain in Trinidad became dissected into little hills and valleys. The flat, senile savanna lands were regenerated, replaced by a younger topography and skeletal soils which could support forest. The trees advanced from the hills and gallery forests and covered the land, so that to-day only a few small relics of savanna on isolated remnants of the old land surface persist as witnesses of Pleistocene conditions.

Davis (1941) has drawn attention to the fact that many of the commonest trees in the rain forests of British Guiana are either endemic or confined to the Guiana region, and put forward the theory that these species were once endemic in groups of islands at

a time when the greater part of the present near-interior peneplain of British Guiana was submerged. When general land conditions returned the island species advanced from their refuges. The flora of the region is essentially local and appears to have received relatively few contributions from Amazonia. *M. excelsa* is not one of the forty common trees considered by Davis, as it is only occasional in the rain forests and he excludes 'the vegetation of coastal and riverine plains and other areas subject to flooding', where mora becomes dominant. The species appears, however, to be endemic to the Guiana region, its known range being the coastal districts of British, Dutch and Venezuelan Guianas (including the Orinoco delta)—and Trinidad, where it is apparently a late arrival. If Davis's theory is correct, *M. excelsa* may well have had an island origin in British Guiana, where it appears as a well-established occasional species in rain forests. When geological uplift took place, mora found suitable conditions to thrive in riverain flats and began rapidly to extend its range laterally along the swampy Guiana coasts. In Eocene, Oligocene and Lower Miocene times the lower-lying parts of Trinidad seem to have been submerged and the Parian ranges of Venezuela, north Trinidad and Tobago would have been separated from Guiana by open sea. In Upper Miocene and Pliocene times this sea shallowed to give rise to muddy, off-shore conditions, and during the Pleistocene stagnation of movement and deposition of sediments brought about a continuous plain from Venezuela right across Trinidad. The Proto-Orinoco then entered the sea somewhat to the eastward of its present mouths. There would at this period have been a direct land connexion between Trinidad and Guiana and an opportunity for the endemic Guianian flora (including mora) to advance towards Trinidad. Actually, few representatives made the journey. Of the forty common Guiana trees detailed by Davis, only two (*Pentaclethra macroloba* and *Eschweilera subglandulosa*) are found in Trinidad, and the former is a species widely distributed in tropical America. It must be remembered, however, that there are no true lowland rain forests in Trinidad for the climate is a seasonal one. Further, during the Pleistocene most of Trinidad was covered with savannas. Opportunities for invasion by rain-forest trees from Guiana would, therefore, have been limited to trees tolerating a fairly considerable range of climatic and other conditions and successful in the low-lying swampy ground of the Proto-Orinoco delta and gallery forests—the avenue by which they must journey. *Mora excelsa* certainly meets these requirements. From the North-West District of British Guiana to the south coast of Trinidad is approximately 120 miles, which at the rate of travel calculated by Marshall for mora would take the tree a million years to cover. Mora seems to have reached Trinidad just as earth movements made it an island. Mora then became cut off from its original home in Guiana, but as forest conditions were returning in Trinidad it was able to establish itself there successfully.

III. CONCLUSIONS

There does not appear to be any reason to question the view that *Mora excelsa* is a recent arrival in Trinidad and that it is in process of invading the evergreen forests in the lowlands. All the evidence points to this conclusion. That it would invade the rain forests in the mountains is doubtful. These forests form a heavy upper canopy at about 90 ft. above ground and are denser and cast a heavier shade than the lowland forests. Since mora appears to have only a limited power in youth of bearing the shade of other species it does not readily colonize dark, dense forests. In the few places where mora has

reached the limits of the 'bois gris' (*Licania ternatensis*) Lower Montane Rain Forest it seems to have made little or no further progress, the boundary being marked by a belt of mixed, co-dominant mora and bois gris beneath which the usual carpet of mora seedlings is noticeably absent. The Semi-evergreen and Deciduous Seasonal Forests of the lowlands seem also hostile to mora, though it has invaded them in places. In this case the dryness of the habitat seems the limiting factor since mora is a moisture-loving species. It is probable that except in the areas of extreme drought mora would invade, though slowly, and would not become so markedly gregarious.

Gunther pointed to the distribution of mora in Guiana as evidence that it would only be likely to colonize, in Trinidad, low-lying, swampy riverain flats. The analogy, however, is a false one. In Guiana, according to the evidence, mora finds its optimum conditions in rain forest where its numbers are limited owing to intense competition: it becomes gregarious on swampy flats in response to lowered competition. In the lowlands of Trinidad there are, strictly, no rain forests (Beard, 1944). There are Evergreen Seasonal Forests which are lower and more open than rain forests and quite clearly offer little or no effective competition to the mora. Mora's great tolerance of a wide range of conditions enables it in Trinidad to colonize successfully and become dominant in a habitat less favourable than its optimum just as in Guiana, though the two sites so colonized in Trinidad and Guiana are by no means comparable. The only comparable case in British Guiana may be in the further interior where mora ascends rising ground and is probably in a zone of seasonal forests.

There is certainly justification for the view that mora reaches its optimum development in Trinidad on riverain flats, for the reason that being properly a rain forest tree it thrives best — in the seasonal climate of Trinidad — where there is most moisture in the soil. Mora is here not confined to such sites though probably it colonizes them more swiftly, and becomes taller and more gregarious upon them.

In order to explain the apparently recent arrival of mora in Trinidad, Marshall appeared to consider that seed must have drifted up on the beach after washing down the Orinoco or Guiana rivers and so have become established. It is true that the beaches of Trinidad are abundantly covered with drift seeds, mainly of *Manicaria saccifera* and *Saccoglottis amazonica*, but the writer has only once found a mora seed among them, and that was so fresh that it appeared to have come from a nearby Trinidad mora forest. In July 1943 Mr J. C. Cater found some mora seeds floating ashore at Guayaguayare Bay, and collected a dozen sound-looking ones which he took home and planted. None germinated. It was presumed that these came from the Orinoco, as no mora were fruiting in Trinidad at the time. Mora seed has a very thin seed coat and it would seem doubtful whether it could withstand prolonged immersion in sea water.

When the recent geological history of Trinidad is considered, a much more likely explanation of the late arrival of mora is discovered. A map of an individual mora forest is shown in Fig. 6, which endeavours to interpret lines of advance. The Mayaro mora forest seems to have spread from land lying to the southward. In late Pleistocene times it may have been already in this vicinity, perhaps in the gallery forests of streams rising in the low hills of this region. Subsequently the mora made its way from the south up to the watershed covered by the 'Mayaro Reserve' (see Fig. 6), crossed it, and travelled rapidly down the streams into the Ortoire and Moruga basins. It will be observed that at the farthest limits of its advance in the west and north-west mora

'tongues out' along the stream flats where it will be advancing most rapidly. Some of the hilly parts, particularly where the forest is of a drier type, have not yet been colonized by the mora. At the rate of advance calculated by Marshall, 50,000 years must have been required for mora to extend from Guayaguayare Bay to its farthest northern and eastern limits, but once it had crossed the Mayaro watershed progress was almost certainly much more rapid and this estimate may be too high.

The Matura mora forest appears to have spread from a point in the vicinity of Saline Bay, either advancing from land lying to the eastward or, less probably, arriving by sea drift. Most likely it advanced up the vega of a stream rising in the Northern Range and flowing south-eastward to join the Orinoco. Some 30,000 years is the probable age of this forest.

The Irois mora forest in Cedros indicates an advance from the west and may have travelled by a land bridge or may have arrived more recently by rafting of seed from the Orinoco during flood. In this case marine dispersal is not so unlikely, since floods of the Orinoco often cast up rafts of driftwood and matted vegetation on this part of the coast of Trinidad—the channel between the delta and Icacos point being only 12 miles wide—sometimes even with living animals upon them. The same applies to the Guapo forest, but the small patch at Cap de Ville, along with the other small and isolated areas in the Nariva Swamp, at Mount Harris and the Aripo valley seem most logically to be due to human influence. The aboriginal Indians in British Guiana are known to use mora seeds as a food, preparing a grated flour or 'farine' from them in a similar manner to cassava. Mora seeds have been shown by analysis at the Imperial College of Tropical Agriculture to have approximately the same food value as maize, though they are not so palatable. The Guiana Indians are said only to use them in case of a shortage of cassava. It seems quite reasonable that wandering hunting parties of these aborigines may have carried supplies of mora seeds on occasion about the Trinidad forests and have abandoned them at camp sites, where they germinated and initiated a new block of mora forest. Since these isolated patches, except that in the Nariva Swamp, are small, the human distribution of the seed need not have occurred long ago—at Marshall's theoretical rate of spread the tree would require only 400 years to cover 2 ha. It seems difficult to envisage the wide distribution of mora seeds by wild animals or birds.

To account for the origin of the 485 ha. of mora forest at Paria Bay on the north side of the Northern Range is admittedly difficult. The forest occupies the bottom of the valley of the Paria river from its mouth to a maximum distance of $2\frac{1}{2}$ miles upstream, which it would appear to have required several thousand years to cover. It is just possible that Indians may have carried the seeds to Paria beach. Otherwise no rational explanation seems possible. This point is the northernmost in the distribution of mora, which is not present in Tobago or Parian Venezuela or the Windward Islands: and it is cut off by the main ridge (600 m. high) of the Northern Range from the Matura forest.

Even when the Pleistocene savannas began to retreat and forest conditions to return, mora must have been a late comer upon the scene. As the grassed plains were dissected forest trees advanced from the hill ranges, monadnocks, sand ridges and gallery forests to which they had been restricted, and if mora had been present we should suppose that it would have advanced with the rest. The *Carapa-Eschweilera* associates, however, were there first. Mora seems to have come up on to the Trinidad land just in time as the surrounding areas foundered. If there were more data as to the exact duration and

extent of land conditions between Trinidad and Guiana during the Pleistocene this matter would probably be clearer.

One final problem remains to be discussed, the gregariousness of *Mora excelsa*. It is an important one, because if the species were not gregarious its invasion of the forests of Trinidad would never have excited comment. It is probable that the distribution of few species is absolutely constant. We should suppose that many species are constantly spreading, others retreating. In Trinidad there are a number of trees whose distribution is limited, apparently only by the time factor. One can cite at random *Saccoglottis amazonica*, *Quassia amara* and *Astrocaryum aureum* confined to the Cedros peninsula and apparently recent arrivals from Venezuela, and *Calliandra guildingii* and *Ryania speciosa*, small trees common on sandy soils only in the north of the island. The distribution of such species excites no particular comment, but the difference between forests with mora and without mora is so striking that it at once seizes the imagination.

It is somewhat misleading to state, as Marshall does (1939), that mora 'forms practically pure crops—in parts absolutely pure crops'. Mora may provide up to 95% of the trees in the upper story, but Table 2 shows the assemblage to contain over eighty-seven component tree species. This does not represent a pure crop in the sense of some northern coniferous forests. The crop, here, is merely one in which a single species is of unusually marked dominance. In this connexion the following comparative figures may be of interest, those at 2, 3, 4 and 11 being taken from Davis & Richards (1933-4), at 5, 6 and 7 from the writer's own records in the Windward Islands, and at 1, 8, 9 and 10 from the Trinidad Forest Department records.

Gregarious forests

| | | % of total individuals | |
Dominant species	Locality	All trees 30 cm. girth and over	Large trees 180 cm. girth and over
1. *Mora excelsa* Benth.	Trinidad	40–60	85–95
2. *Mora gonggrijpii* Kleinh.	British Guiana	26	61
3. *Ocotea rodioei* Schomb.	British Guiana	9	43
4. *Eperua falcata* Aubl.	British Guiana	21	67
5. *Dacryodes excelsa* Vahl.	Dominica	10	13
6. *Dacryodes excelsa* Vahl.	Grenada	35	75
7. *Amanoa caribaea* Urb.	Dominica	20	45

Mixed forests

| | | % of total individuals | |
Principal dominants	Locality	All trees 30 cm. girth and over	Large trees 180 cm. girth and over
8. *Carapa guianensis* Aubl.	Trinidad	9	21
Eschweilera subglandulosa (Steud.) Miers.		2	3
9. *Licania ternatensis* Hook.f.	Trinidad	10	9
Sterculia caribaea R.Br.		7	18
10. *Licania biglandulosa* Gr.	Tobago	16	5
Byrsonima spicata (Cav.) Rich.		5	20
11. *Eschweilera*, four species, together	British Guiana	13	18
Licania, three species, together		22	18

There is no hard and fast distinction between a 'gregarious' forest and a 'mixed' forest. The distinction is merely a matter of degree of abundance of the dominants, and this is very variable among both types. Among the seven gregarious types listed above

there is a variation by the dominant from 10 to 60% of the crop, and a like variation may occur within associations, as evidenced by the difference between the *Dacryodes excelsa* types in Dominica and Grenada. In parts of the mountains of Trinidad *Licania ternatensis* (type 9) may, locally, attain 30% of the crop.

It is by no means uncommon to remark the gregariousness or high abundance of a single species in associations in adverse habitats, e.g. in swamps and high mountain areas, where adversity decisively limits the flora to few species. The forest types under discussion here lie, however, close to the optimum. It is possible that immaturity of the flora is an important factor. Davis believes the Guiana peneplain flora to be of recent development and of endemic, island origin. Trinidad is an island, whose forest flora may be immature due to the recent return of forest conditions. The writer's examples above of *Dacryodes* and *Amanoa* forests are from islands. The gregariousness of a species may thus be due to the lack of vigorous competitors. In Dominica where there is a much richer flora *Dacryodes excelsa* is less highly gregarious than in Grenada.

Dominance is evidently decided by a number of different factors, notably suitability of the species to the site, production of seed, power of seedlings to bear shade and competition, the latter comprising the density, vigour, stature and reproductive power of the associates.

Mora appears to be, in the part of Trinidad where it is so far found, to be at least as well suited to conditions as any of the local species. Its production of seed is phenomenal, as is also the percentage germination of its seeds. The seedlings readily bear the shade cast by the crappo-guatecare forests, but themselves cast a far heavier shade. It must be a matter of difficulty for any seedling other than a mora to come up through the dense mass of mora saplings. The species thus establishes initially a thick ground carpet of its own seedlings which maintain an almost exclusive right to succession in the forest. Once such a carpet has been laid down it is only a question of waiting for the older trees to die before a gregarious mora forest comes into being.

Gunther drew attention to the difference in stature and structure between mora and other forest, as shown by aerial survey. The same is vividly demonstrated by the profile diagrams (Figs. 2, 3). The stratification is comparable, but mora, being gregarious, forms canopy at a higher level—the level reached by the average mature tree. A forest of gregarious crappo or guatecare would clearly adopt the same structure as mora forest. In both types there are three strata, but in mora forest the uppermost forms canopy and in mixed forest the middle one. Certain typical species in the crappo-guatecare forest attain the upper story or the middle, or are confined to the lower story. This behaviour is observed also in mora forest, but these species, of course, become much reduced in numbers and are subordinate to the mora.

IV. SUMMARY

The mora forests of Trinidad in which *Mora excelsa* Benth. is dominant and gregarious occupy certain restricted areas.

No environmental factors appear to account for the alternation of mora forest and mixed crappo-guatecare (*Carapa-Eschweilera*) forest.

Mora is believed to be a recent arrival in the island and to be actually invading the mixed forests.

Mora is of wide distribution in Guiana, where it is occasional in most types of rain forest, becoming gregarious only on swampy flats where competition is lessened.

Mora is believed to have crossed over to Trinidad from Guiana by a land bridge in late Pleistocene to subrecent times.

Mora is thought to have become gregarious in Trinidad because the moist forests are not typical rain forests, but have a more open structure. Shade is sufficiently thin to enable mora readily to become established, after which its great reproductive power makes it gregarious and its greater height suppresses the mixed forest.

REFERENCES

Beard, J. S. (1944). Climax vegetation in tropical America. *Ecology*, **25**, 127–58.

Berry, E. W. (1925). *Studies in Geology*, **6**, 71–161.

Davis, T. A. W. (1929). Some observations on the forests of the North-West District. *Agric. J. Brit. Guiana*, **2**, 157–66.

Davis, T. A. W. (1941). On the island origin of the endemic trees of the British Guiana peneplain. *J. Ecol.* **29**, 1–13.

Davis, T. A. W. & Richards, P. W. (1933–4). The vegetation of Moraballi Creek, British Guiana. Parts I and II. *J. Ecol.* **21**, 350–84; **22**, 106–55.

Gunther, A. E. (1942). The distribution and status of mora forest (*Mora excelsa*) in the Ortoire Basin, Trinidad. *Emp. For. J.* **21**, 123–7.

Hollick, A. (1924). A review of the fossil flora of the West Indies. *Bull. N.Y. Bot. Gdns*, **12**, 259–323.

Marshall, R. C. (1934). *The Physiography and Vegetation of Trinidad and Tobago.* Oxford Forestry Memoirs **17**.

Marshall, R. C. (1939). *Silviculture of the Trees of Trinidad and Tobago.* Oxford.

Key to Index Letters on Profile Diagrams (figs. 2 and 3).

Abbreviations	Local Name	Scientific Name
A.	"Arena" Sardine	*Pera arborea* Mutis
B.	Blackheart	*Clathrotropis brachypetala* (Tul.) Kleinh.
B.c.	Bois chandelle	*Amaioua corymbosa* H.B.K.
B.ch.	Bois charbon	*Diospyros ierensis* Britton
B.l.	Bois l'agli	*Ryania speciosa* Vahl.
B.m.	Bois mulatre	*Pentaclethra macroloba* (Willd.) Kuntze
B.p.	Bois pois	*Swartzia pinnata* Willd.
B.t.	Bois tatou	*Rudgea freemani* Sprague and Williams
C.	Crappo	*Carapa guianensis* Aubl.
Ca.	Cajuca	*Virola surinamensis* (Rol.) Warb.
Cb.	Carimbo	*Guarea glabra* Vahl.
Coc.	Cocorite	*Maximiliana elegans* Karst.
Cp.	Cooperhoop	*Brownea latifolia* Jacq.
G.	Guatecare	*Eschweilera subglandulosa* (Steud.) Miers
Ga.	Gasparee	*Esenbeckia pilocarpoides* H.B.K.
In.	Incense	*Protium guianense* (Aubl.) March
L.s.	Laurier stinker	*Ocotea arenaensis* R. L. Brooks
La.	Laylay	*Cordia* sp.
M.	Mora	*Mora excelsa* Benth.
Ma.	Mahoe	*Sterculia caribaea* R. Br.
Me.	Manac	*Euterpe langloisii* Burret
Mk.	Milkwood	*Sapium aucuparium* Jacq.
Mi.	Sardine	*Miconia* sp.
N.	Niauré	*Calliandra guildingii* Benth.
P.	Poui	*Tabebuia serratifolia* (Vahl.) Nichols
P.d.	Pois doux	*Inga* sp.
S.	Soiebo	*Rheedia* sp.
W.	Wakamy	*Warszewiczia coccinea* (Vahl.) Kl.
W.c.	Wild cocoa	*Tovomita eggersii* Vesque
W.co.	Wild coffee	Rubiaceae sp.
W.o.	White olivier	*Terminalia amazonia* (J. F. Gmel.) Exell.
Y.o.	Yellow olivier	*Buchenavia capitata* (R. and P.) Steud.

THE BIPHASIC OR SOIL-WATER CULTURE METHOD FOR GROWING ALGAE AND FLAGELLATA

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(With two Figures in the Text)

CONTENTS

I. INTRODUCTION

Progress in microbiology, as a result of the adoption of pure-culture methods, has been so striking that in the opinion of some biologists a culture not free of bacteria is not a real culture at all. The statement that bacteria-containing cultures of various kinds may be of use, and the enumeration of successive stages in the attempt to obtain pure cultures (Pringsheim, 1926, p. 287), has, for this reason, led to misunderstandings.

To-day, after many more years of research in this field, I can emphasize that uni-algal cultures containing a certain amount of bacteria are in more than one respect a suitable basis for investigation. They are often not merely a preliminary to the production of pure cultures but, if based on ecological considerations, they may also be the best approach to the biology of a form. The matter in question is therefore of more than technical importance. Without cultures originating from single cells, progress along diverse lines would be arrested, and the elucidation of many problems of algal physiology, taxonomy and ecology would take place far more slowly than would be possible with the help of the method described in these pages.

One often meets with a few algal cells or filaments which are of special interest but cannot be identified for one or more of the following reasons: scanty representation, absence of reproductive stages, quick movement, the necessity of performing micro-chemical tests, of applying stains or utilizing special optical equipment. Such obstacles to detailed investigation may be encountered every time they are observed.

It may be argued that forms which are only represented by a few individuals are unimportant, but such scarcity may be misleading. The individuals may be concentrated round a particular spot, e.g. a decaying worm, within the habitat. If a certain quantity of water and mud is gathered, the forms inhabiting ecologically different micro-habitats become mingled with one another.

In fact biological investigations have often hitherto been restricted to species occurring in relatively dense communities, a condition which may never be realized in nature in the case of various species. This was so with the Astasiaceae, most species of which remained unrecognized until single-celled putrefaction cultures were prepared (Pringsheim,

1936, 1942). These proved to be the only means of obtaining genetically homogeneous material on which a diagnosis could be based, so long as growth in the absence of bacteria could not be achieved. Klebs (1883, p. 290) states: 'Für diese farblosen Formen ist characteristisch, dass sie nur dann in grösserer Menge auftreten, wenn organische Massen in Fäulnis übergehen. Sie zeigen im Anfang einer Infusion sich nur in einzelnen und schlecht genährten Exemplaren, vermehren sich in wenigen Tagen bei steigender Fäulnis in zahlloser Menge,...bis sie nach kurzer Zeit fast spurlos wieder verschwinden....In freier Natur findet man daher nur selten diese farblosen Euglenen, sie werden erst bemerkbar in Zimmerkulturen.' Similar conditions obtained in relation to *Trachelomonas*, the specific limits of which could not be defined until genetically uniform material was available. In other instances adequate investigations have depended on the chance discovery of a species in large quantities. Some species of *Euglena* and *Cryptomonas* generally occur as a few scattered individuals, and many more examples are found in the relevant literature.

Earlier papers (Pringsheim, 1921, 1936, 1942) have described a method in which media, containing soil and water, have been used to secure abundant growth of any species of the Astasiaceae desired. It also rendered possible the differentiation and description of forms which had previously been inadequately characterized owing to their occurrence in a specialized habitat and their capacity for morphological modification. A similar technique had been previously used by Jacobsen (1910) and the writer (1921) for enrichment cultures of Volvocales and Cryptomonadaceae, especially of their saprophytic members.

Attempts to increase the availability of such methods for growing small organisms have proved successful. The results can only be published gradually, because in each case time is required to discover the best modification of the general method, and to describe the organisms thus grown from the morphological and physiological points of view. It may be useful to give meanwhile an account of the technique that has been developed during the last five years.

The processes described in these pages do not lead to pure, i.e. bacteria-free cultures. As previously emphasized (Pringsheim, 1926, pp. 287–8), pure cultures, though indispensable for solving certain problems, are not necessary for many others. A special publication (Pringsheim, 1945), in which I deal with pure culture methods, will show that I do not neglect them in algal research. It was just the experience detailed in that book which led me to the conclusion that, when working with bacteria-free cultures, the conditions necessary for the healthy growth of a form are often difficult to discover and to create so that other methods may be preferable.

This is not only due to our restricted knowledge or poor technique in preparing suitable media, but quite as much to the fact that a clear, sterile solution cannot always provide in sufficient quantity every compound or element necessary for abundant growth. Some chemical elements ($Fe^{...}$, Si, P) are precipitated under certain conditions, or they may be poisonous ($Fe^{..}$) if not very dilute, and the same applies to certain organic compounds, for instance fatty acids, otherwise suitable as nutritive substances (Provasoli, 1937–8, p. 80). In nature much larger quantities of water are available per individual than in thriving cultures and dissolved substances are generally replenished from bottom deposits which contain insoluble or colloidal or adsorbed substances with which we are not yet sufficiently familiar. For these reasons lack of nutrients is more likely to affect

organisms in a restricted quantity of culture medium than in their usual habitats (cf. Mortimer, 1941, with extensive bibliography).

When dealing with monophasic media, i.e. clear, sterile solutions, little can be done to meet nutritional requirements by the employment of more soluble or less poisonous compounds of indispensable elements. Such chemical or physical devices do not offer sufficient possibilities of variation. They can, however, be supplemented by biochemical means, imitating nature's example, where the setting free of stored food from bottom deposits is mostly effected by bacterial activity. Conditions are thus created whereby algae, flagellates and other small organisms, which it is desired to cultivate, take up nutritive substances provided by the bacteria living in the mud phase.

Competition or confusion with similar forms, need not be feared if culture tubes are heated before inoculation in order to destroy germs of algae, flagellates, fungi, etc., which are present in the soil, although bacterial spores are not completely killed. The essential value of the type of cultures described in this paper lies in the properties of the bottom layer of 'mud' in contact with the culture solution proper. This bottom deposit provides relatively large quantities of food material which gradually diffuse into the liquid medium. Soil is generally the only or the chief component of the bottom deposit so that the technique can be described as the *soil-water culture* method. By varying the kind of soil and adding diverse substances, adaptation to the special needs of different organisms can be achieved but some multiplication is usually obtained with a standard medium of garden soil and water.

The results show that cultural possibilities are greatly increased as compared with the usual monophasic nutrient media. The improvements concern not only the number of organisms which can be cultivated, but also the quality and quantity of the material grown and the longevity of the individual cultures.

There are five biological groups of micro-organisms, differing in their mode of nutrition, which may advantageously be grown in soil-water cultures:

(1) Chlorophyll-containing photo-autotrophic or 'holophytic' organisms.

(2) 'Saprophytic' organisms devoid of assimilatory pigments and living on dissolved organic compounds.

(3) 'Holozoic' organisms, likewise containing no chlorophyll and living on solid food particles, usually bacteria or other small organisms.

(4) 'Hemizoic' organisms, occasionally devouring solid food, but at the same time possessed of chromatophores with chlorophyll.

(5) 'Mixotrophic' organisms which, though containing assimilatory pigments, do not grow properly without dissolved organic compounds.

It is necessary also to distinguish polytrophic habitats which abound in the organic (as well as inorganic) substances on which saprophytic, mixotrophic, holozoic and hemizoic organisms thrive. Habitats containing an abundance of inorganic nutritive salts are termed *eutrophic* in contrast to the nutritionally poor oligotrophic type.

II. Preparation of Culture Vessels

For most purposes test-tubes are sufficient. Hard glass, such as Jena or Pyrex glass, is preferable to the softer varieties because it does not affect the pH of the contents and is not readily corroded. Thick-walled tubes should be employed because the heavy unyielding soil at the bottom facilitates breaking when the tubes are placed in a container

or otherwise strained. For special purposes larger tubes, glass cylinders or milk bottles are useful. They are handled in essentially the same way as test-tubes.

In order to prevent excessive putrefaction, organic substances supplying food materials are placed at the bottom of the vessel and covered with soil. This is one of the roles of soil in this technique. Substances, which are primarily insoluble, are preferable to such as are readily dissolved because disintegration is gradual and food materials are progressively placed at the disposal of the cultured organism.

The choice lies between nitrogen-containing proteins on the one hand and carbohydrates on the other.

Casein, gelatine and similar substances constitute an appropriate source of nitrogen and carbon compounds. Fragments of dried cheese are very effective in creating polytrophic conditions, but the formation of ammonia results in an alkaline reaction which is not always desirable. Mixtures of proteins and carbohydrates are usually more suitable. Seeds and grains of cereals, such as wheat or barley, afford natural mixtures of this kind. The quantity can be varied by using smaller or larger grains or more than one. Single grains of pearl barley yield enough organic food for a test-tube culture of any polytrophic green form, although colourless saprophytes need more for abundant growth.

Plain starch is often the most suitable material. Anaerobic fermentation leads to the formation of fatty acids which are neutralized by the addition of calcium carbonate, likewise placed at the bottom of the tube. The nitrogen content of fertile soil seems to suffice for the plentiful multiplication of many organisms, for instance of most species of Astasiaceae and Polytomaceae.

The organic substances are put into the tube, with or without the addition of compounds affecting the pH of the culture fluid. Next follows a column, 3 or 4 cm. high, of soil, usually ordinary garden soil, which has been dried and sifted. It should not contain too many decaying organic particles, which would cause excessive putrefaction or mycelium formation in the overlying culture fluid. The kind of soil can be varied according to requirements. Many organisms prefer surface soil from arable land which is usually poorer in humus than that of gardens.

Apart from the humus content and reaction, other properties, such as nitrogen content, etc., also influence the result, but for most purposes any kind of soil, if not newly manured, can be used. Leaf-mould and various kinds of peat, composed of *Sphagnum*, fern or root remains, are suitable only when an acid medium is required. Peat, covered with soil, often promotes a better growth than either ingredient used separately. We dispose therefore of a wide range of possible combinations which can be tested in individual cases. A set of three to five tubes, containing for example ordinary soil with distilled water, soil with $CaCO_3$, a cereal grain with soil and peat with soil, will usually suffice to afford a first insight into the ecological adaptation of a given chlorophyll-containing alga or flagellate. Water is added to cover the dry substances to within 5 cm. of the rim of the tube, so that it does not reach the cotton-wool plug. Tap water can be used if it is not chlorinated or so hard as to influence the pH in an undesirable way; in all other cases distilled water should be employed. Each investigator will introduce slight modifications of his own.

The tubes are then heated to destroy unwanted organisms. They should, however, not be placed in a hot steam chamber or allowed to reach the boiling-point, since such treatment often causes soil and water to rise to the top of the tube with consequent

wetting and soiling of the plugs. It is safest to heat the steam chamber with a small flame for at least 3 hr. No real sterilization is intended.

III. ISOLATION AND INOCULATION

One of the advantages of the technique here described is, that the organisms to be cultivated are selected and separated from other forms at the outset. Inoculation is effected by picking up single cells, filaments, coenobia, etc., under a binocular microscope with a magnification of 40–80 diameter and transferring them to a prepared culture tube. Free-swimming flagellates, zoospores, etc., are more readily recognized than non-motile individuals so that smaller cells can be taken up, down to those which are only $10–12\mu$. For still smaller cells a micro-manipulator is indispensable.

In picking up the organisms required capillary pipettes or glass needles are used. The latter are employed to lift filaments or fragments of branched algae. In general, however, pipettes, drawn out to form very fine capillaries with a bore of about $50–100\mu$, are more suitable. As a preliminary, ordinary glass pipettes, 30 cm. in length, are prepared from 4 mm. bore tubes, drawn out to $\frac{1}{2}–1$ mm. bore. These are provided with small cotton-wool plugs at the wider end, which in addition is surrounded with cellulose wadding or tissue paper to form plugs that will fit into test-tubes (Fig. 1). After autoclaving, the pipettes can thus be kept sterile inside and outside for an indefinite period. Before they are used for selecting specimens under the microscope the narrow ends are heated over a small flame and, after removal from the source of heat, drawn out into fine capillaries. They are broken off into suitable lengths by exerting a sudden longitudinal pull with a forceps. A circular opening is thus made without any risk of contamination. A single pipette can be drawn out repeatedly and so used several times. Capillary pipettes may not be sterilized by heating after they have been finally shaped.

Fig. 1. Sterile pipette in test-tube, as employed for the aseptic transference of drops of culture fluid and for making capillary pipettes.

Living cells with a small quantity of water are sucked up into the pipette by capillary force. The opening of the pipette is watched under the microscope as it approaches the object to be taken up and, immediately after this has passed into it, the latter is lifted out of the water. The same procedure can be repeated until ten or even more cells have been taken up with a single pipette so as to provide sufficient material for the inoculation of a number of media. The fine and elongate capillaries employed can only be emptied by the operation of considerable pressure, and ordinary thin rubber caps will not suffice for this purpose. A piece of pressure tubing, closed at one end by a glass plug, serves it better. Even so some seconds elapse before the column of water is emptied from the capillary into another fluid.

As containers for the sterile washing fluid watch-glasses are used. They should have a diameter of 5–6 cm. and be shaped so as to form part of a regular sphere. Flattened ones are not suitable because the few drops of liquid employed would not remain in the centre as they should. The watch-glasses are put into closed Petri dishes and sterilized by dry heat at 160–170°C. for $1\frac{1}{2}$–2 hr. The watch-glasses are supported on wire triangles, best

made of aluminium (Fig. 2); these prevent displacement. The optical conditions could probably be much improved, and the recognition of algal cells facilitated by using a condenser beneath the stage and glass containers of a special form. Owing to war-time conditions such devices could not be tested.

In order to wash the cells a number of watch-glasses are supplied with about 6–8 drops of sterile fluid. Mere water is often unsuitable because harmful to the cells. As a rule dilute mineral solutions, or soil or peat extract are better. Their *p*H must be adapted to the needs of the organism.

The cells or filaments to be used for starting soil-water cultures are not transferred directly from the original fluid to the culture. The risk of mixed inoculation, resulting from

Fig. 2. Sterile watch-glass, supported by wire triangle in Petri dish.

the presence of small organisms other than bacteria, would be too great. It is, however, unnecessary to repeat the washing process as often as in making pure cultures (Pringsheim, 1945, p. 71). To avoid contamination of the cultures with small algae like *Chlorella, Coccomyxa, Scenedesmus* or minute Cyanophyceae the cells to be used for inoculation should be passed through a sterile fluid at least twice. A series of three or four watch-glasses, each containing sterile fluid introduced with a sterile pipette, is therefore needed. The first is provided with a quantity of the original algal mixture.

Several cells may be handled at the same time without emptying the capillary when a specimen has been sucked in, and the same capillary can be used for the entire series of washing transfers. If, however, the tip becomes soiled by adhering mucilaginous matter, it must be shortened or drawn out afresh to provide a clean tool and to avoid contamination by organisms adhering to the outer surface of the capillary.

If only a few or but a single specimen of the required species can be found, isolation is often nevertheless possible, although the risk of loss then renders washing inadvisable. The cell or cells are therefore transferred directly to a soil-water culture of a type most likely to be suitable to their needs and, when the first signs of multiplication are observed, the material thus obtained is used for the preparation of several secondary cultures by picking up single cells in the usual way. Cultures have thus been raised from single cells on several occasions.

From the last watch-glass, individual cells or filaments are used for inoculating cultures. If an appropriate medium has been found, single cells will usually give rise to cultures. If, however, there is reasonable certainty that individuals of different species are not included, it is safer to transfer several cells to each tube. This is specially advisable when a species is being dealt with for the first time, and the suitable kind of culture medium is not yet known. Single-cell or clone cultures are thus deferred until the conditions for reliable multiplication have been ascertained. Such clone cultures should, however, never be neglected if taxonomic descriptions or physiological research are to be based on homogeneous material.

Until special skill in employing the above technique has been acquired, there may sometimes be difficulty in distinguishing the required species under the binocular microscope. When this is so, the organism should be examined successively under high power, under medium magnification and under low power, before using the binocular microscope. Under low power note is taken of its shape and size, of its visual appearance, and, in
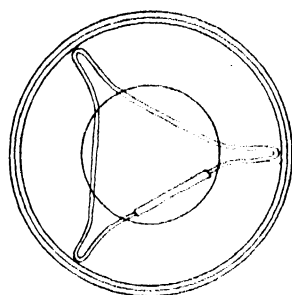
flagellates and zoospores, of its manner of moving, so that confusion with other organisms becomes improbable.

A difficulty may result from cessation of movement when the organism is transferred to another medium. In such instances the organism may appear undisturbed in the first watch-glass, although during the subsequent transfers active movement ceases and an unhealthy appearance is acquired. This difficulty can often be overcome by keeping the material for a day in a mixture of equal parts of the original fluid and of that to be used in the process of isolation by washing. Then more of the washing fluid is added, and thus the organisms are accommodated to it, before the actual process of isolation commences.

IV. CULTURAL CONDITIONS AND OBSERVATION OF RESULTS

The conditions to which cultures are exposed, depend on the needs of the species concerned. Organisms containing chlorophyll are kept in the light, while colourless forms may be reared in the dark unless it is proposed to conduct feeding experiments with green algae.

Cultures, exposed to the light, are best placed or suspended near a north window during the brighter season of the year (Richter, 1911; Pringsheim, 1926, p. 292). At other times, i.e. from September till March, the intensity and duration of natural illumination is insufficient, judging by my experience in Prague and Cambridge. The illumination must therefore be supplemented by artificial light or the latter used exclusively. In the former case electric bulbs are grouped inside the room near the window so that the cultures receive additional illumination apart from the daylight. The bulbs also cause a slight rise of temperature, which may be advantageous because slow development during winter seems to be due to low temperature, as well as to insufficient illumination. For the same reason the culture vessels should not touch the window panes.

It is usually stated that algal cultures should not be exposed to direct sunshine, and as a rule this warning is justified. In nature, however, algae are sometimes found exposed to insolation. In early spring and late autumn at least, cultures often thrive better at a west or east or even a south than at a north window. They can be protected from the effect of too intense radiation by sheets of tissue paper. When the cultures show considerable growth, they are transferred to a cooler place with dim illumination, for instance a north window in an unheated room, and numbers of them are kept in large jars with paper lids.

For the provision of a more constant source of illumination, full artificial light is indispensable. It is only in this way that comparable cultural results can be obtained. A single large bulb of 400 or 500 W. is more economical than several smaller ones of, say, 50 W. Using ten of the latter, illumination nowhere much exceeds that between two bulbs only, while it is approximately five times as strong at a certain distance from a 500 W. lamp as at the same distance between two 50 W. lamps.

The effective light radiation from such a large bulb can only be properly utilized if a cooling screen of water is interposed to prevent overheating and drying out of the cultures; otherwise they would have to be placed so far from the source of light that the intensity would be insufficient. In order to obtain a fairly constant illumination the lamp and its water-screen should be placed in a dark room.

A simple illumination device consists of a 500 W. lamp, surrounded by continually running water. It need not be in operation during the whole 24 hr.; 8-12 hr. are

sufficient. Algae, which would sooner or later grow on the inner surface of the vessel, would appreciably reduce the light intensity, but this can be remedied by separating the water-screen from the cooling system. Tap water is allowed to flow through a coiled copper pipe arranged above the source of light, so that the screen of distilled water, poisoned by a little copper sulphate, is indirectly cooled by the tap water (Pringsheim, 1926, p. 309; 1945, pp. 83 et seq.). Regarding the devices used for suspending culture tubes and exposing them to natural or artificial light, see Pringsheim (1926, pp. 292–3; 1945, p. 86).

The time needed for a culture to develop from a single cell into an evident population depends on temperature and light intensity, as well as on the composition of the medium. Under equal conditions it takes much longer than takes a subculture started with a larger quantity of living material, although this is not the only reason for differences between single-cell and mass-inoculation cultures. The latter often lead to a more plentiful and healthier growth. The best time for microscopic investigation is commonly during the period of a few days or weeks after heavy inoculation, for later the individuals may be full of reserve substances. Young plants of filamentous algae may be present in large numbers after mass-inoculation, while the later stages may not develop at all owing to competition.

Many soil-water cultures keep for half a year or longer, if placed in a cool and dimly lighted place. The greatest danger is evaporation of the surface fluid, leaving the algae as a dry ring; complete desiccation usually results in the death of the whole culture. Even the concentration of the culture fluid by evaporation is dangerous. This can be prevented by adding sterile water, but it is more convenient and efficacious to reduce evaporation by covering the opening of the tube. The simplest device consists of a disk of 'wax-paper' (impregnated with solid paraffin) and kept in place by a rubber band or a ring of gummed paper; cellophane or ordinary paper can also be used. A cap of tin-foil, fastened to the tube by insulation tape, is almost completely air-tight and preferable to a rubber cap which becomes brittle under the influence of light. Caps of this kind should not be applied before the culture has reached a sufficient development, since they completely sever the connexion between the inner and outer air which is not so if paper is used.

Aspects of the growth of micro-organisms in cultures, which cannot be properly observed with the naked eye, are often detectable with a hand lens, especially if inspected against a frosted electric bulb. Observation under a low-power microscope of the contents of a tube is also possible to a certain extent, and often very helpful. The disturbing optical influence of the cylindrical surface of the culture tube can be reduced by attaching a coverslip to it with a drop of glycerine.

For microscopical investigation under high power, drops of the culture fluid from that region in which the organisms live are removed with a sterile pipette. Emphasis should be laid on the value of hanging-drop preparations and dark-ground illumination, with which every student of micro-organisms should be familiar. Much confusion has arisen from the exclusive investigation of preserved material or fixed and stained preparations, which often cannot be adequately interpreted without simultaneous observation of living material. It is often useful to watch motile cells in a hanging drop, while subjected to iodine-, osmic- or formalin-vapour. For this purpose the coverslip is fixed to the hollowed slide by a minute drop of water, so that another drop, containing the volatile reagent can be added with a loop when the organisms, first observed in the living state, are to be fixed.

V. RANGE OF POSSIBILITIES AND DISCUSSION

The technique described in the preceding pages is easily applied but, if the best use is to be made of it, it must be adapted to meet special needs. The range of possibilities is wide and attractive. On the one hand we have the algae of oligotrophic waters, e.g. lakes with rocky bottoms. On the other hand we have the organisms found in localities where there is plentiful decay of organic substances, and where, as a consequence, there is competition with bacteria and manifold Protozoa. Soil-water cultures afford the possibility of creating conditions suitable for the growth of both and of almost every other kind of micro-organism.

By using a soil, poor in humus and other organic remains, together with glass-distilled water, the conditions found in oligotrophic waters can be imitated. The concentration of dissolved substances can be varied by using different amounts of soil. Addition of low concentrations (0·001-0·01 %) of mineral nutritive solutions provides conditions suitable to organisms which are a little more pretentious and renders the growth richer and more prolonged. The substitution of peat for soil makes the medium both acid and rich in humus, while the concentration of nutritive salts remains low. Various kinds of peat (cf. p. 196) have a different effect.

The conditions obtaining in the natural habitat should always be taken into consideration. The whole method is an ecological one, imitating the circumstances prevailing where the organism occurs and often more fully defining them when they are little known. Cells of a given species should consequently be inoculated into various media. The diversity can consist in the use of different kinds of soil and in varying its quantity in relation to the water. Up to a certain point the pH can be varied by using different kinds of soil, by adding peat or calcium carbonate and so on. Further possibilities lie in the addition of organic substances (cf. p. 196) capable of putrefaction, thereby influencing the amount of soluble carbon compounds, the pH, the O_2- and CO_2-tension, the quantity of bacteria, etc. Organic substances, added to the soil, are indispensable for saprotrophic flagellates, e.g. *Chilomonas*, *Astasia*, *Polytoma*, while holozoic Chrysomonadaceae and other flagellates are so modest in their requirements that they multiply in mere soil-water cultures with garden soil, the organic substances present sufficing for enough bacteria to feed upon. There are, on the other hand, quite a number of chlorophyll-containing organisms which multiply more copiously, if supplied with a small quantity of putrefiable material. The presence of small grains of cereals at the bottom of a tube with soil and water has a favourable influence on the development of certain green species of Euglenaceae and Chlamydomonadaceae.

Not all the chemical elements required by micro-organisms are present in sufficient quantity in every soil from a garden or a cultivated field. This is borne out by comparison with cultures containing additional inorganic nutritive substances, which sometimes have a favourable influence. Fe and Mn are generally available in an amount sufficient for *Trachelomonas* but not for all flagellates with iron and manganese deposits. *Anthophysa*, *Siderodendron* and biologically similar forms may therefore excrete conspicuous stalks only if more Fe and Mn are provided than are contained in the soil.

A complete list of the organisms so far grown in serial soil-water cultures over a longer period as 'persistent cultures' (Allen & Nelson, 1910, p. 424) would occupy too much

space, but the following examples may be mentioned to illustrate the wide range of possibilities.

Iron and purple bacteria, *Zoogloeae* and *Spirilla*, all of which are not readily grown in pure cultures, are common in raw cultures inoculated with mixed material from nature where such forms live. They can be raised at will and cultivated indefinitely. Some Chrysophyceae, most of which have hitherto scarcely been grown in cultures, multiply readily from single cells or coenobia. Among them are *Ochromonas*, *Chromulina*, *Synura*, *Uroglena*, *Dinobryon* and the apochlorotic genera *Monas*, *Oikomonas*, *Anthophysa*. The same can be said concerning colourless flagellates of doubtful allegiance, such as *Naegleria* (syn. Dimastigamoeba), *Bicosoeca*, *Poteriodendron*, *Desmarella* and others, as of many Ciliates. Volvocales and Cryptophyceae almost all multiply well. Dinophyceae are difficult to grow, although two or three of the few species tested throve abundantly. This is also true of all green and colourless Euglenineae, with the exception of certain holozoic forms, for only few of which suitable living conditions could so far be provided. Little experience has been collected regarding Diatoms, but some of the fresh-water and marine forms grew very well. Cyanophyceae, such as *Oscillatoria*, *Phormidium*, *Pseudanabaena*, *Merismopedia*, *Chroococcus*, *Synechococcus*, *Anabaena*, *Nostoc*, etc., also for the most part grew exceedingly well. Many species of Chlorococcaceae, Scenedesmaceae, Ulotrichaceae, Oedogoniaceae and Chaetophoraceae are easily cultivated by this means. Several species of *Vaucheria* were grown in soil-water cultures from isolated zoospores, which proved to be the only way of excluding other algae, and afforded normal and healthy material showing the same features and kinds of reproduction as in nature. Of Conjugales *Spirogyra* and *Mougeotia*, as well as Desmidiaceae and Mesotaeniaceae, throve in such cultures. I have so far little experience with seaweeds. On the whole, organisms which could not be grown with the methods described are exceptions.

The opinion that appreciable progress has been achieved by the soil-water culture technique, is based on the following considerations:

(1) It seems probable that it will soon be possible to cultivate almost every free-living alga or flagellate as well as other small organisms, such as ciliates, worms, larvae of larger animals, etc. Most of the species hitherto investigated have grown more abundantly and healthily than in other types of cultures. Biphasic cultures persist longer than monophasic cultures with nutritive solutions and are superior to the latter for most purposes, except in relation to the study of the actual physiology of nutrition.

(2) The conditions of life in such cultures for the most part resemble those found in nature. The course of the life cycle and complexities of morphological structure can often be followed up more completely than in the original habitat.

(3) By singling out individual cells, coenobia or filaments and using them as the starting-points for cultures, the population of a piece of water can be analysed. The various species isolated are protected from competition, which would eliminate most of them if they were left together under laboratory conditions. When a fraction of a natural population is removed from its habitat, its composition changes in a few days or even hours, either owing to the lack of special nutritive compounds or the accumulation of bacteria or other rapidly growing micro-organisms. The first-named effect prevails under oligotrophic, the latter under polytrophic conditions. The addition of a mineral nutritive solution or of single salts is not very helpful, since it tends to favour

the more rapidly growing and readily adaptable forms to the detriment of specialized ones which are often more interesting.

(4) By varying the ingredients in biphasic cultures the optimum combination of conditions can be discovered, and valuable information obtained concerning ecological adaptation. Although the cultural media employed are of a complex nature, their utilization constitutes a nearer approach to the solution of ecological problems than can be attained by the use of monophasic media, because the conditions more nearly resemble those in the original habitat, while growth is more prolonged and less disturbed by changes in the medium.

(5) When algae, flagellates and other small organisms are grown in soil-water cultures they flourish for a longer period than they would in the original medium under laboratory conditions. They can thus be used at leisure for morphological investigations, for demonstration and class-work and for starting new cultures.

Although developed only four years ago the soil-water technique has already been widely used though not yet systematically explored. It is to be hoped that further investigations will lead the way to other improvements, so that it may become possible to grow a still larger variety of organisms, including more of those whose culture has so far proved difficult or impossible. Such are the forms found in waters with an extreme paucity of nutritive elements, or those which require other special organisms as a source of food. In the first case the difficulty lies in the rapid exhaustion of the very dilute nutritive solutions to be used, not so obvious in nature because of the low density of the population throughout the habitat. The difficulty of growing such oligotrophic organisms in sufficiently large numbers for detailed investigation, can be overcome by employing nutritive substances of low solubility which are only slowly used up. Soil-water cultures, with their two phases, are helpful also in this respect.

Forms depending on solid organic food particles mostly feed on living microorganisms; they can often be supplied in cultures with the latter, as has been done with flagellates, amoebae and ciliates. Organisms supplied as food in a medium which favours their multiplication, however, often tend to grow too rapidly and may overwhelm the forms which they are supposed to sustain. On the other hand, transference to an indifferent medium affording no nourishment for the food organisms leads to their rapid elimination, as a combined result of starvation and of serving as a source of food. The problem, therefore, becomes one of equilibrium between the feeding organism and that which supplies food, which, in nature, is the basis of their mutual existence. To a certain extent this difficulty can be overcome by using dilute media or such as are not too favourable, but soil-water cultures with their capacity to supply nutritive substances over long periods would often appear to be the better, or even the only satisfactory device.

VI. SUMMARY

A simple technique is described, with the help of which many micro-organisms have been grown in culture for the first time or more successfully than has hitherto been possible. It consists in using culture vessels containing soil, sometimes with the addition of nutritive substances, and water, and heated so as to destroy most of the germs present. Isolated cells, coenobia or filaments are inoculated and in general multiply more healthily and vigorously than in the cultural media hitherto employed.

REFERENCES

Allen, E. J. & Nelson E. W. (1910). On the artificial culture of marine plankton organisms. *J. Mar. Biol. Ass. U.K.* **8**, 421.

Jacobsen, H. C. (1910). Kulturversuche mit einigen niederen Volvocaceen. *Z. Bot.* **2**, 145.

Klebs, G. (1883). Ueber die Organisation einiger Flagellatengruppen. *Untersuch. Bot. Inst. Tübingen*, **1**, 233.

Mortimer, C. H. (1941). The exchange of dissolved substances between mud and water in lakes. *J. Ecol.* **29**, 280.

Pringsheim, E. G. (1921). Zur Physiologie farbloser Flagellaten. *Beitr. allgem. Bot.* **2**, 88.

Pringsheim, E. G. (1926). Kulturversuche mit chlorophyllführenden Mikroorganismen. V. Methoden und Erfahrungen. *Beitr. Biol. Pflanz.* **14**, 283.

Pringsheim, E. G. (1936). Zur Kenntnis saprotropher Algen und Flagellaten. I. Ueber Anhäufungskulturen polysaprober Flagellaten. *Arch. Protistenk.* **87**, 43.

Pringsheim, E. G. (1942). Contributions to our knowledge of saprotrophic algae and flagellata. III. *Astasia, Distigma, Menoidium* and *Rhabdomonas*. *New Phytol.* **41**, 171.

Pringsheim, E. G. (1945). *Pure Cultures of Algae, their Preparation and Maintenance.* Cambridge.

Provasoli, L. (1937-8). Studi sulla nutrizione dei Prozozoi. *Boll. zool.* **8**, 3.

Richter, O. (1911). *Die Ernährung der Algen.* Leipzig.

OBSERVATIONS ON THE COLONIZATION OF BARE CHALK

By G. H. LOCKET

(With Plate 10 and one Figure in the Text)

In view of the fact that not many records have been made of the colonization of bare chalk, it was felt that the following observations, begun in 1933, on the latest of the Harefield (Middlesex) series of chalk pits (abandoned in 1929), were worth putting on record.
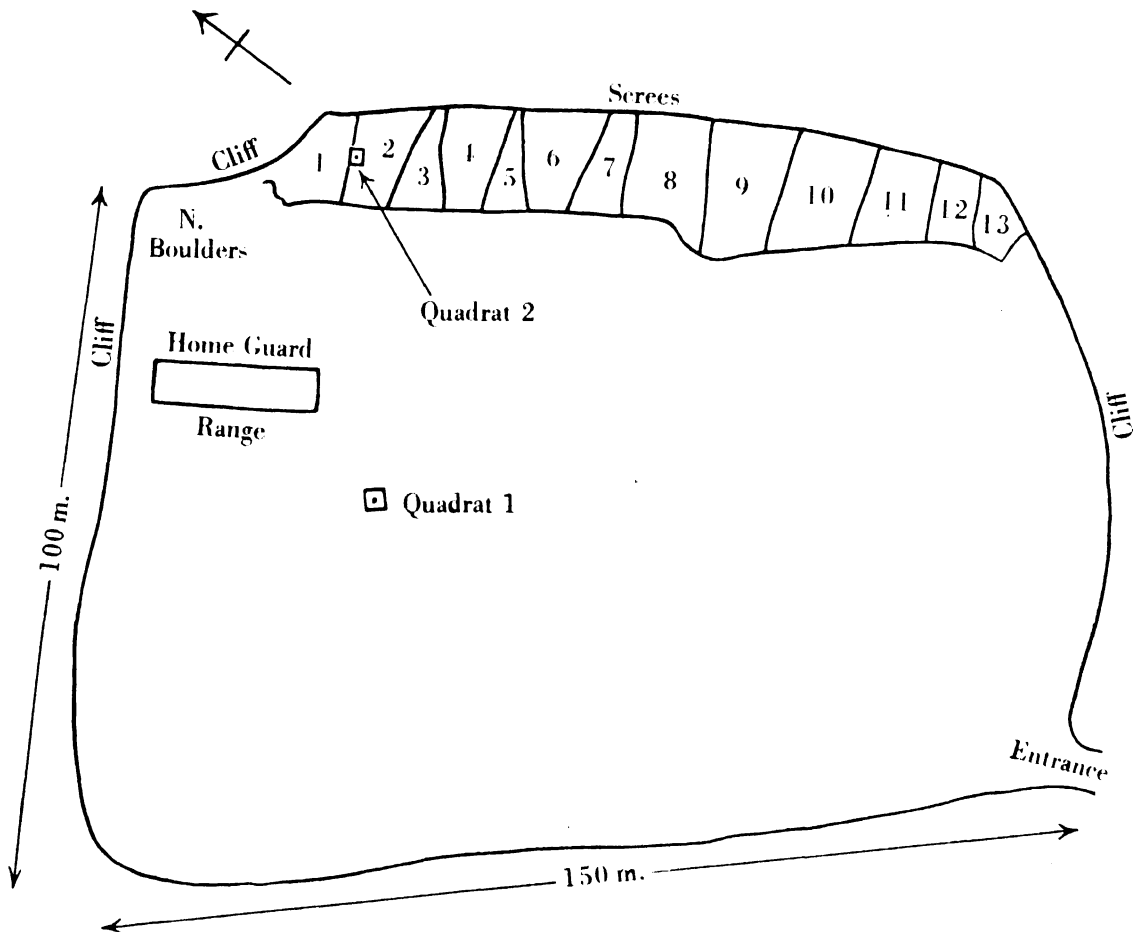
Fig. 1.

The region investigated consists of an oblong pit (Fig. 1) measuring about 150 by 100 m. It is some 15 m. deep at the upper and 10 m. deep at the lower side and is cut in the side of the hill sloping from Harefield to the Grand Union Canal. Colonization was studied on the floor of the pit and on the slopes along the north-east side from which chalk had been won. The slopes (35–40° to the horizontal) were divided from each other by ridges and covered with unstable chalk scree; they are referred to as the

'screes'. Some boulders at the base of a cliff at the north corner are called the 'North boulders', and an interesting small area was provided in 1940 by the construction of a 25 yd. range by the Home Guard, leaving the chalk bare. The chalk is overlaid here by a 4–6 ft. stratum of Woolwich and Reading beds (sand and gravel), hence the surrounding flora is by no means typical of chalk.

Half-metre quadrats were started in 1933 on the floor and on Scree 2. For counts and records Scree 4 was selected as typical.

It seems very likely that we have here an extreme case of the type of colonization discussed by Hope-Simpson (1940) which he considers should occur in the absence of rabbit grazing, namely, progress to woodland without intermediate formation of a stable herbaceous association. (In the Harefield pit rabbit grazing is very light.)

WOODY PLANTS

In the floor area *Salix caprea* and *S. cinerea* with *Betula alba* were the precursors, the former two species showing signs (1943) of having reached their limit of growth at some 12 ft. high. *Acer pseudoplatanus*, *Crataegus monogyna*, *Fraxinus excelsior* have become well established more recently as well as *Quercus robur*. All colonize the bare chalk without any difficulty and have spread throughout the area. The trees (now mostly destroyed by the military) in the older workings included *Salix caprea*, *Fraxinus*, *Ulmus*, *Aesculus hippocastanum*, *Acer pseudoplatanus* and *Crataegus*, but even here it is very doubtful if any real stability had been attained. *Rubus* sp. occurs but has not grown to an extent which makes it important as yet.

On the screes the same *Salix* and *Betula* spread and grew rapidly in spite of severe attacks by rabbits in the winter 1933–4. They exploit the pulverized top soil and their main roots run horizontally for a distance approximating to the height of the trees. As the soil moves down the slopes these roots become bared and the *Salix* tends to die when about 6–8 ft. high. *Betula*, exploiting more the lower crevices, survives better. *Crataegus* occurred in 1933 and has increased slowly, being found frequently in 1943. The conditions for the survival and increase of *Clematis vitalba* are not clear. On Scree 4 the numbers of this plant in 1937, 1939, 1940 and 1943 were 16, 48, 36 and 19 respectively. Local dominance in parts of the older workings was temporary.

HERBACEOUS PLANTS

In July 1933 the whole floor area was dominated by *Melilotus officinalis* growing 2–3 ft. high, then in full bloom. The following year showed a marked decrease, but in 1935 there was again an increase (though not to the 1933 level) to be followed in 1936 by an unprecedented decrease. In 1937 an increase again occurred to be followed by a steady decline in numbers (except for a slight increase in 1940). By 1942 it was hard to find plants in the pit. The fluctuations up to 1937 may well be due to the biennial habit, and a precisely similar fluctuation was obtained by sowing a bare bank of clay at Harrow. Drought does not appear to be a serious factor. The seeds germinate quickly and are viable for at least 7 years, but *Melilotus officinalis* cannot withstand competition, being ousted at Harrow in 3–4 years by grasses. It is interesting to note that it flourishes in east Yorkshire on cliffs which are constantly eroded, thus exposing new soil surfaces. Rabbits were not found to attack it in the chalk pit and cannot have played much part

in its disappearance. *Lotus corniculatus* was abundant throughout the floor area, and it was not seen to be attacked by rabbits, although severe frost (1939–40) damaged it. Preferentially, it exploits crevices well below the upper weathered chalk, leaving the latter to *Medicago lupulina*, *Festuca ovina* and *F. rubra*. The *Medicago* is a very rapid colonizer of bare chalk but is susceptible to drought and soon loses its local dominance. The fescues flourished exceedingly in the absence of rabbit attacks after 1940; they were highly susceptible to drought but always increased steadily after colonizing bare chalk very readily. In 1933 a mat of dead fescue was found at the south-west end of the pit mixed with the living plants. Decomposition was slow owing to drying out until, by 1942, with the accumulation of *Brachythecium purum* and *Eurhynchium praelongum* and weathering of the chalk, an organic layer was accumulating in the top 2 in. of soil. *Arrhenatherum elatius* was a colonist of first-rate importance which established itself wherever crevices were available, and it also exploits the weathered top soil. Although invading a new area less quickly than *Festuca* (it was frequent but nowhere dominant on the Home Guard range after 2 years), yet it has quickly become abundant everywhere and there has been no record of its decrease, nor of attacks by rabbits. It was locally dominant in some of the older workings, and doubtless it will always compete successfully as long as crevices are available for its roots. For instance, though it was frequent on the screes by 1943, it was abundant on the loose chalk boulders below.

For the rest the following observations speak for themselves.

Plants colonizing the Home Guard range (cleared and abandoned in 1940)

	1941	1943		1941	1943
Achillea millefolium	o.	o.	Medicago lupulina	o.	l.d.
Agrostis stolonifera	.	o.-f.	Pimpinella saxifraga	.	f.
Arrhenatherum elatius	f.	f.-a.	Plantago media	.	o.
Artemisia vulgaris	.	o.	Populus sp.	.	r.
Avena pubescens	.	o.	Ranunculus bulbosus	o.	o.
Betula alba	o.	f.	Reseda luteola	l.a.	Not found
Bromus erectus	.	o.	Rosa canina	.	1 pl.
Centaurea nigra	.	o.	Rubus fructicosus agg.	.	o.
Chrysanthemum leucanthemum	o.	o.	Rumex acetosa	o.	o.
Cirsium lanceolatum	o.	f.	R. crispus	.	2 pls.
Clematis vitalba	.	1 pl.	Salix cinerea and caprea	r.	f.
Crepis biennis	o.	f.	Scrophularia nodosa	o.	f.
C. taraxacifolia	.	o.	Senecio erucifolius	o.	r.
Dactylis glomerata	o.	f.	Sonchus oleraceus	o.	o.
Daucus carota	o.	o.	Taraxacum vulgare	o.	f.-a.
Epilobium angustifolium	.	o.	Trifolium pratense	.	r.
Festuca rubra and ovina	o.	a.	Tussilago farfara	o.	f.
Heracleum sphondylium	o.	o.	Veronica chamaedrys	.	o.
Hieracium pilosella	.	l.a.	Vicia sativa	.	f.
Hypericum perforatum	o.	f.-a.			
Leontodon hispidus	.	o.	Bryum capillare with		
Lotus corniculatus	.	o.	Barbula fallax	.	a.

Numbers of plants in characteristic 0·25 sq.m. quadrats

Quadrat 1. Counts of *Lotus corniculatus* were made on the emergent stems from which branches came. Rabbit grazing was never severe but continuous until 1940–1, when all rabbits disappeared from the area. The results are considered to be wholly typical of this part of the floor area.

	1933	1934	1936	1937	1938	1939	1940	1943
Agropyron repens	.	.	.	.	.	1	.	.
Agrostis stolonifera	.	.	.	.	.	.	.	1
Arrhenatherum elatius	.	.	.	3	2	.	3	15
Crepis capillaris	1	.	.	.	.	.	.	.
Dactylis glomerata	.	2	.	.	.	.	3	12
Daucus carota	2	2	13	8	7	14	9	16

Number of plants in characteristic 0·25 *sq.m. quadrats* (continued)

	1933	1934	1936	1937	1938	1939	1940	1943
Fragaria vesca	.	.	.	.	.	.	.	3
Geranium sp.	.	.	.	.	.	.	.	1
Holcus lanatus	.	.	.	1	.	4	.	.
Linaria minor	1	.	.	.	.	.	.	.
Linum catharticum	.	.	2	.	2	.	12	11
Lotus corniculatus	2	5	23	21	24	25	21	22
Malva sylvestris	.	.	.	1	.	2	1	.
Medicago lupulina	13	5	4	9	11	8	12	10
Melilotus officinalis	.	.	1	1	.	.	1	.
Pimpinella saxifraga	.	.	.	.	.	.	.	12
Rosa canina	.	.	.	.	.	.	1	.
Salix cinerea or caprea	1	.	.	.	.	.	.	1
Taraxacum sp.	.	1	.	.	.	.	.	.
Tussilago farfara	4	1	1	.	.	.	.	.

Quadrat 2. After 10 years the area is still quite open, being now overshadowed by a *Salix* bush. The coming and going of *Clematis vitalba* is clearly shown; it was no nearer to being established in 1943 than in 1934. *Hypericum perforatum*, on the other hand, showed an increase after 1941 and this happened all over the screes area. Two specimens of *Cirsium lanceolatum* survived for 4 and 5 years respectively without producing flowers. One individual of *Agrostis stolonifera* survived for 6 years. '*Crepis*' seedlings probably include *C. capillaris*, *C. taraxacifolia* and *Taraxacum* sp. '*Leontodon*' seedlings are at least *L. hispidus* and *Hypochaeris radicata*.

	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943
Agrostis stolonifera	.	.	.	1	1	1	1	1	1	1
Artemisia vulgaris	.	.	1	1	1	.	.	.	.	.
Chrysanthemum leucanthemum	.	.	.	.	2	2	.	1	.	.
Cirsium lanceolatum	2	2	2	2	2	1	.	1	1	.
Clematis vitalba	3	4	3	6	7	4	3	4	2	3
Daucus carota	.	.	.	.	.	.	1	.	.	.
Fraxinus excelsior	.	.	.	.	1	1	1	2	1	1
Heracleum sphondylium	.	.	.	.	.	.	.	.	.	2
Hypericum perforatum	.	.	.	.	.	.	1	.	3	6
Malva sylvestris	.	.	.	1	.	2	1	2	1	.
Reseda luteola	1	.	.	.	.	.	.	.	.	.
Salix cinerea or caprea	.	.	.	.	.	.	.	.	1	1
Scrophularia nodosa	.	.	.	.	.	2	.	.	.	.
Senecio erucifolius	.	2	2	1	1	1	2	1	.	1
Tussilago farfara	.	1	.	.	1	.	.	.	.	.
'Crepis' seedlings	10	3	1	6	3	1	1	3	.	.
'Leontodon' seedlings	1	4	2	3	6	6	3	4	2	1

Area Scree 4. The sudden disappearance of *Plantago lanceolata* from the top of the screes in 1943 is very curious, since no landslide sufficient to account for it has occurred.

The symbol ' + ' indicates that the plant was present occasionally. The absence of a symbol means that the plant was not found.

The species asterisked chiefly colonize the loose soil at the top of the screes.

	1934	1937	1943		1934	1937	1943
Acer pseudoplatanus	.	.	3	*Lotus corniculatus	37	v.a.	l.d.
Betula alba	1	+	16	Melilotus officinalis	50	+	.
Centaurea nigra	.	37	>200	*Plantago lanceolata	+	140	+
Chrysanthemum leucanthemum	66	59	10	Quercus robur	.	2	6
Cirsium lanceolatum	.	+	1	Ranunculus bulbosus	.	.	f.
Clematis vitalba	.	16	19	Reseda luteola	22	21	.
Crataegus monogyna	.	.	3	Rosa canina	.	.	2
Crepis capillaris	34	.	.	Rumex acetosa	18	+	2
C. taraxacifolia	.	.	f.	Salix cinerea and caprea	2	?	13
Daucus carota	.	.	f.	Scrophularia nodosa	2	4	.
Epilobium angustifolium	17	+	6	Senecio erucifolius	.	+	f.
Fraxinus excelsior	.	+	29	Tussilago farfara	9	+	1
Hieracium pilosella	.	.	l.a.	Veronica chamaedrys	.	+	l.a.
Holcus lanatus	.	+	.	Vicia sativa	.	+	+
Hypericum perforatum	.	+	29				
Lathyrus pratensis	+	+	5	Dactylis glomerata	.	+	.
Leontodon hispidus	5	r.	.	Poa pratensis	.	+	.
Linaria minor	a.	f.	.				

a

b

Observations on the colonization of bare chalk: the Harefield chalk-pit from the
same view-point (*a*) in 1937, (*b*) in 1943.

The occurrence of plants not otherwise recorded

	Locality	1934	1937	1940	1943
Acer campestre	Floor area		.	o.	o.
Agrimonia eupatoria	Floor area	.	o.	r.	r.
Anacamptis pyramidalis	Floor area	o.	o.	o.	f.
Artemisia vulgaris	Floor area and screes	o.	o.	o.	o.
Barbarea vulgaris	Floor area	f.	f.	o.	.
Brachypodium sylvaticum	North boulders	f.	f.	a.	l.d.
Briza media	Floor area	o.	o.	o.	o.
Bryonia dioica	North boulders	f.	f.	f.	f.
Centaurea scabiosa	Floor area	.	.	r.	r.
Dipsacus sylvestris	Floor area	f.	r.	r.	.
Epilobium hirsutum	North boulders	o.	o.	o.	o.
Fumaria officinalis	Floor area	o.	o.	o.	r.
Galium erectum	Floor area	.	.	.	1 pl.
Heracleum sphondylium	Floor area	1 pl.	o.	o.	l.a.
,, ,,	Screes	.	.	.	o.
Hieracium pilosella	Floor area (3 patches)	.	l.a.	l.a.	l.a.
Orchis maculata	Floor area	o.	f.	f.	l.a.
Origanum vulgare	Floor area (1 patch)	.	1 pl.	l.d.	l.d.
Poa pratensis	Floor area (probably overlooked earlier)	.	.	.	o.
Potentilla anserina	North boulders	.	l.f.	l.f.	l.f.
Poterium sanguisorba	Floor area	.	.	r.	.
Primula veris	Floor area	o.	l.a.	l.a.	l.a.
Ranunculus repens	Floor area	.	.	.	l.a.
Rubus fructicosus agg.	North boulders	f.	f.	l.a.	l.d.
Senecio jacobea	North boulders	l.a.	f.	r.	.
Sonchus arvensis	Floor area	r.	r.	r.	r.
Tragopogon pratensis	Floor area and screes	.	.	.	o.
Trifolium repens	Floor area (1 patch)	.	.	.	l.d.
Vicia cracca	North boulders	o.	o.	o.	o.

Dr Richards (1928) records other mosses from the area (see p. 207), but he warns me that the list may not be complete.

There is little doubt that throughout the whole area water supply is a most important factor, and an attempt will be made to throw light on the problem in a second paper.

In conclusion I wish to express my best thanks to Prof. E. J. Salisbury for suggestions and practical help, to Dr P. W. Richards for identifying the mosses, and for help from members of the Harrow School Natural History Society, especially from D. Burnett.

REFERENCES

Hope-Simpson, J. F. (1940). Studies of the vegetation of the English chalk. VI. *J. Ecol.* **28**, 386.
Richards, P. M. W. (1928). Ecological notes on the bryophytes of Middlesex. *J. Ecol.* **16**, 290

A CONSIDERATION OF *JUNCUS EFFUSUS* L. AND *JUNCUS CONGLOMERATUS* L.

By R. D. TWEED AND N. WOODHEAD, *University College of North Wales, Bangor*

Early in 1942 Prof. Pearsall told us of his observations on the British distribution, horizontal and vertical, of *Juncus conglomeratus* L. and *J. effusus* L., and said that in his opinion the critical points of distinction between these two species were not yet generally comprehended. Since then our own observations in Wales have confirmed his opinions on the distribution, and our survey of recent literature certainly suggests confusion between these Junci.

The separation of Meyer's *J. communis* into these species in the field has apparently been based upon the simple morphological character expressed by their specific names, the former being applied to those with a compact inflorescence, and the latter to those with a spreading inflorescence. The reason for this is not hard to seek, as many of the standard British floras particularly emphasize the character of the inflorescence, whether *J. communis* Meyer is used to cover both species, or whether they have been separated into *J. conglomeratus* L. and *J. effusus* L. Graebner (2) goes so far as to write that the two species cannot be distinguished unless fruits are available. It is important to bear in mind that the two species are separated chiefly by differences in the capsule and stem. These points are fairly stated in the brief analysis introducing each species in the 'Biological Flora of the British Isles' (6), where also a passing reference is made to the frequent confusion between them: some of the subsequent information in this 'Flora' is so contradictory that the confusion due to the nomenclature may well increase rather than diminish.

The 'Biological Flora' refers to a variety of *J. effusus* with a compressed inflorescence, incorrectly cited as var. *congestus* Lej. & Court. It should properly be referred to as *J. effusus* L. var. *compactus* Hoppe (= *J. effusus* L. var. *subglomeratus* Lam. & DC.). Lejeune & Courtois (4) made no mention of a variety '*congestus*'. The nomenclature is the subject of a separate paper by the present writers, for there has been a long history of continued wrongful citation.

The 'Biological Flora' has not taken into account the very widespread distribution of this variety, so often mistaken for *J. conglomeratus*. It is our experience that no reliance can be placed on records of *J. conglomeratus* for North Wales unless there is a clear expression that cognizance has been taken of the variety. Search over the four counties, Anglesey, Caernarvon, Denbigh and Merioneth, leaves us with the conclusion that *J. conglomeratus* is a very rare plant within their bounds.

The scheme on p. 211 portrays the main contrasts between the two species, and the corresponding characters of the variety for comparison.

In passing, the Welsh specimens of ripe seeds do not agree with Buchenau's measurements (1), which, in turn, were not in conformity with later published data. The statements in the 'Biological Flora' that the seeds of *J. effusus* are yellowish is not borne out by examination of ripe seeds from Welsh specimens, nor by the descriptions in continental Floras, etc.

	J. effusus	*J. effusus* var. *compactus*	*J. conglomeratus*
Axis	Faintly striate with 40–90 striation, smooth to the touch	Similar to *J. effusus*	Conspicuously striate with 20 or less striations, rough to the touch
Fruit	Retuse, not apiculate. Colour olivaceous	Retuse, not apiculate. Brownish, darker at tip	Truncate, apiculate. Brownish, darker at tip
Perianth segments	Green with broad scarious margin	Variable in colour, but usually more or less intermediate between the two species	Reddish, with green centre
Leaf sheath	Not inflated	Not inflated	Inflated
Seeds	Reddish brown, approx. size 0·47 × 0·21 mm. Number per capsule 50–100	Yellow, approx. size 0·53 × 0·19 mm. Number per capsule 50–100	Yellow, approx. size 0·58 × 0·21 mm. Number per capsule 50–90
Anthers	Oval, about as long as the filaments	—	Strap-shaped, nearly as long as the filaments

The summary of altitudes given on p. 376 of the 'Biological Flora' does not seem to create a clear impression of the distributional features of these plants. There is much reason to believe that *J. effusus* is generally much more frequent in this country at higher altitudes.

The information on p. 382 is so contradictory that some of the altitudes given must be suspect for *J. conglomeratus*. If the species is abundant in the north and west, it can only be so below 1000 ft., for Pearsall's experience is that it rarely occurs above that level. Where the species are separated in ecological literature it is almost always *J. effusus* that is abundant or dominant, e.g. among the Sphagneta of the northern Pennines and Cornwall (Tansley (8), pp. 697, 698). Little emphasis can be placed upon those rush communities in the fens of Lough Neagh, for Tansley's statement itself ((8), p. 666) implies a doubt concerning the actual identity of the 'common rush' there present. Moss (5) makes no mention of *J. conglomeratus* communities in the Pennines but states that 'The rush (*Juncus effusus* and *J. effusus* forma *compactus*), in damp places, and independently of conditions of shelter or exposure, is an abundant and characteristic associate. The bracken and the rush, in fact, are, in many places, harvested by the upland farmers.' It is significant that in his list of species of *Juncus* swamps these abundant communities do not include *J. conglomeratus*. Of the two species, *J. effusus* is decidedly the commoner dominant. In Snowdonia it is an extremely abundant plant.

In North Wales, our difficulty has been to find any specimens of *J. conglomeratus* at all, even at low altitudes. Two localities were found in the Conway Valley, one in a larch plantation at Gelli, Crafnant, near Trefriw, at a height of about 600 ft., the other near Penmachno, somewhat below that height. A third locality was in Cwm Gwara, near Clynnog-fawr, south of Caernarvon. In every case the distribution was patchy and rare among an abundance of other rush species. The extensive areas dominated by rush in the mountains of North Wales have *J. effusus* L. var. *compactus* Hoppe as the dominant species, which, as has already been pointed out, can easily be mistaken for *J. conglomeratus*. The list on p. 212, which is by no means exhaustive, but indicative of the very wide range of locality and altitude occupied by the plant, gives an impression of the wide search made. The variety was abundant or dominant in every case.

The Migneint area corresponds roughly with the example quoted in the 'Biological Flora' 'on Silurian slates of central North Wales near Bala' for *J. conglomeratus*. It seems most likely that the plants were actually *J. effusus* var. *compactus*.

Few county Floras mention this variety, though many we have examined make the

Juncus effusus L. var. *compactus* Hoppe

Locality	County	Altitude (ft.)	Collector
Llangeinwen	Anglesey	10	D. Thoday
Malltraeth	,,	20– 50	,,
Llyn Coron	,,	30	,,
Valley	,,	50	H. Jacob
Portmadoc	Caernarvon	0– 50	R. E. Hughes
Aber	,,	100	Authors
Ogwen	,,	200– 600	,,
Nant Ffrancon	,,	600–1100	,,
Nant Gwynant	,,	200– 700	,,
Llanberis, and Snowdon Path	,,	500–1000	,,
Hafod y rhedrwydd	,,	1400	,,
Pont Nant y lladron	Merioneth	1300–1450	,,
Migneint moors	,,	1000–1400	,,
Ffynnon Eidda	,,	1600	,,
Bangor	Caernarvon	50	,,
Pentre voelas	Denbigh	750	,,

All these records have been checked by the present authors.

point that *J. conglomeratus* is less common than *J. effusus*. The altitudinal lists on p. 382 of the 'Biological Flora' are not necessarily inaccurate, but those taken from Floras which have not discriminated the compact variety of *J. effusus* from true *J. conglomeratus* are suspect, e.g. those of west Lancashire and Breadalbane. Our own observations in North Wales are certainly at variance with the quoted examples.

In the North Wales counties *J. effusus*, species and variety, have an extensive distribution on the mountain slopes, poor pastures retrogressive to moorland, and in the more open parts of woods. In effect, the association on higher ground is dominated by the variety, which forms conspicuous clumps of considerable density, and may be so abundant that wide areas, amounting to many acres, appear sere and brown over long periods of the year: here, we do not see the 'yellowish green' appearance mentioned in the 'Biological Flora'. The upland Junceta effusi compacti examined by us, between 750 and 1600 ft., are characterized by a rich moss flora and but few phanerogams. *Eurhynchium praelongum* Hobk. is the most widely spread of the concomitants.

Juncetum effusi compacti

Juncus effusus var. compactus	d.	Sphagnum cymbifolium	a.
J. articulatus	o.	Hylocomium splendens	a.
Galium saxatile	o.	Polytrichum commune	a.
Agrostis alba	o.	S. cuspidatum	a.
Chrysosplenium oppositifolium	o.	S. acutifolium	f.
Eurhynchium praelongum	v.a.		

At lower altitudes, in the upper limit of oak-birch wood on the steep mountain slopes, *J. effusus* societies comprise a richer phanerogamic flora, but the mosses remain abundant. The following list is typical:

Juncetum effusi typici

Juncus effusus	d. (large plants)	Mentha aquatica	
Galium saxatile	f.	Circaea lutetiana	
Filipendula ulmaria		Stellaria uliginosa	
Cardamine flexuosa		Eurhynchium praelongum	v.a.
Epilobium palustre		Hypnum cupressiforme	a.
Holcus lanatus		Campylopus pyriformis	f.
Ajuga reptans			

Some *p*H determinations (electrometric) are now available for North Wales; those for

J. effusus lie within the range given in the 'Biological Flora'. Those for the variety range from pH 3·67 to 6·22. We are indebted to Dr Margaret Baecker for these determinations.

We have also been able to fill in some of the gaps in the 'Biological Flora' for *J. effusus* and its variety. Both species are anemophilous. Reports of occasional entomophily are of little value without reference to the insect visitors observed. Neither species showed a mycorrhizal infestation. Most capsules had shed their seeds by the end of November, and in both cases a high proportion of the seeds showed a circular hole bored through the wall by some predatory creature. In one case an acarine was discovered in a capsule on dissection. Where capsules had not been attacked, and the seeds had not been disseminated, the number of seeds varied between 50 and 100. In the section on 'Performance in various habitats' attention may be drawn to F. R. E. Wright's paper (9), where it is stated (p. 266): 'Among the Rushes, *J. acutus*, *maritimus*, and *effusus*, which are all tall, with unbranched, aphyllous stems, show no alteration of form or stunting.'

It is apparent from the foregoing that the ecology of the two species and the variety still requires considerable revision. We have noticed, in addition, omissions from the text of the parts of the 'Biological Flora' for *J. inflexus* L. and *J. subnodulosus* Schrank. In the first, Salter (7) had recorded *J. inflexus* for Cardiganshire in six localities, in one in great abundance. Hyde & Wade's *Welsh Flowering Plants* (3) contains similar information. The statement at the head of p. 370 should therefore be deleted. Easterness should, of course, be vice-county (96), not (97). For *J. subnodulosus* a record for Renfrew, v.c. 76, by R. Mackechnie in 1933 can be added; the *Bot. Soc. Exch. Rep.* for 1933 states that it had been recorded in the Topographical Botany but not in the Comital Flora.

The writers wish to express their thanks to E. M. Cutting, Esq., for his kindly advice and criticism.

REFERENCES

(1) **Buchenau, F. (1867).** Die Skulptur der Samenhaut bei den Deutschen Juncaceen. *Bot. Ztg.* **25**, 201.

(2) **Graebner, P. (1909).** Juncaceae. In *Lebensgeschichte der Blütenpflanzen Mitteleuropas,* ed. Kirchner, Loew, Wangerin and Schröter.

(3) **Hyde, H. A. & Wade, A. E. (1934).** *Welsh Flowering Plants.* Cardiff.

(4) **Lejeune, A. L. S. & Courtois, R. (1831).** *Compendium Florae Belgicae,* 2. Leodii.

(5) **Moss, C. E. (1913).** *Vegetation of the Peak District.* Cambridge.

(6) **Richards, P. W. & Clapham, A. B. (1941).** *Juncus effusus* and *Juncus conglomeratus* in 'Biological Flora of the British Isles'. *J. Ecol.* **29**, 375.

(7) **Salter, J. H. (1935).** *Flowering Plants and Ferns of Cardiganshire.* Cardiff.

(8) **Tansley, A. G. (1939).** *British Islands and their Vegetation.* Cambridge.

(9) **Wright, F. R. E. (1932).** Alterations in vegetative growth due to environmental adaptation in Braunton Burrows. *Bot. Soc. Exch. Club Rep.* **10**, 258.

SOME FACTORS AFFECTING THE DISTRIBUTION OF THE CAPREAE GROUP OF *SALIX* IN GOWER

By JOHN WILKINSON, *University College, Swansea*

(*With one Figure in the Text*)

Whilst engaged upon an investigation of *Salix* from a cytogenetical point of view, the results of which are recorded elsewhere (Wilkinson, 1944), the writer had the opportunity of looking into the occurrence and distribution in Gower of the chief naturally occurring species and hybrids of this genus. The prevalence in this area of the species and, more particularly, the hybrids, of the subsection Capreae of *Salix* was found to be particularly striking, and it was thought worth while to attempt to elucidate some of the factors involved in the distribution of this group. The following short account summarizes the results which have been obtained.

The Gower Peninsula, which extends approximately 20 miles west of Swansea, is geographically a plateau with an average elevation of about 250 ft., the surface being dominantly limestone but carrying a thin veneer of drift. Above the plateau level there stand ridges of Old Red Sandstone, as at Cefn Bryn and Rhossili Downs; and below it there are depressions, for the most part deeply eroded in or upon Millstone Grit, such as the valleys at Oystermouth and Oxwich. Some of the valleys are not so formed. Thus, the valleys leading to Caswell and Three Cliffs run along faults, and those at Bishopston and Ilston are 'dissolved' valleys in limestone. Whatever their mode of formation, the valley walls are characteristically steep, so that the low-lying valley floors are usually near to regions of high elevation at plateau level. This is of particular importance in connexion with the occurrence and distribution of certain of the Capreae species and hybrids.

A brief consideration of the geological structure of Gower, particularly in relation to soil production, is desirable for a proper appreciation of problems of *Salix* distribution. The Old Red Sandstone formation is the oldest, and appears as bare quartz conglomerate rock in the highest areas, with an inherent tendency to be slightly acid in nature. The soils resulting from the downward migration of 'hill wash' after continual weathering are of poor quality and support only the peaty *Eriophorum-Sphagnum* moorlands which are distinctly acid, pH values of 3·5–4·5 being typical.

Next in geological sequence comes the Limestone, which, except for certain beds which are fairly highly magnesian or dolomitic, is very pure on the whole, and gives rise to no soil at all except in lowland regions where it rests upon the Old Red Sandstone. Such regions (e.g. Burry Green and Pennard) are calcareous and waterlogged, the calcareous content being sufficient to ensure their alkalinity, so that pH values of 7·2–7·5 or more are encountered. Most of the Limestone of the southern part of the peninsula, being very porous, is well drained.

The Millstone Grit, which is virtually the youngest rock series in Gower (the Trias is so scantily represented as to be negligible), is almost wholly represented by fine-grained,

DISTRIBUTION OF CAPREAE IN GOWER

Fig. 1.

Caprea C
aurita .... A
atrocinerea .... A
aurita x Caprea .... aC
aurita x atrocinerea .... aA
Caprea x atrocinerea X
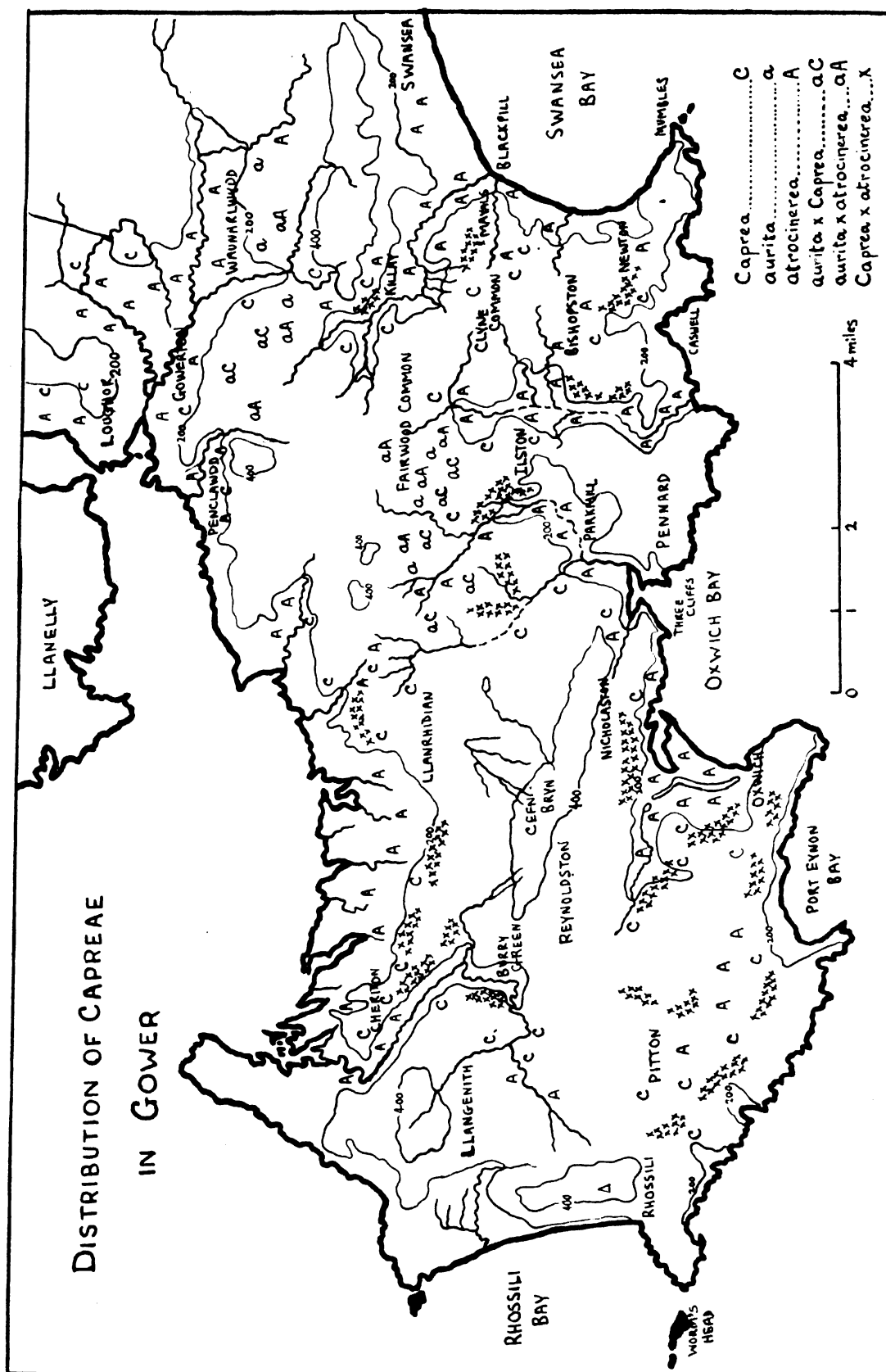
impervious shale. This is soft, easily eroded, and forms acid soils conspicuously lacking calcareous material; drainage is bad, because of the impervious nature of the substratum. Typical situations are the depressions at Oxwich and Newton. At Oxwich, drainage is worsened by the damming of the valley mouth by sand-dunes.

Apart from the effect of the solid geology, the nature of the soil of Gower also depends upon the widespread presence of superficial glacial drift. The whole of the peninsula was originally blanketed with ice, and glacial deposits occur almost everywhere. Due to the fact that most of the ice moved from Central Wales and mingled with drifts of Irish Sea origin in this area, these are for the most part very mixed, and are composed of sands, gravels and clays of polygenetic origin. There is an almost entire lack of calcareous constituents, and even where the drift is only a few feet deep the soil is unaffected by a calcareous foundation. In those situations where the glacial clay components of the drift, as distinct from sand and gravels, thin out upon the Limestone, the soil possesses an appreciable calcareous content, and the calcareous material is leached out relatively slowly. The leaching of drift composed of gravels and sands is very rapid. Some of the best farm lands of Gower are found in those regions where abundant glacial drift rests upon a pervious foundation, such as at Mayals and upon the mounds above Oxwich Green, Port Eynon and Rhossili. In those regions, however, where the drift is potentially good but rests upon an impervious foundation of Millstone Grit, as at Oxwich Marsh and the region north of Cefn Bryn, the land is markedly acid and of little value for farming.

A record of the broad features of taxonomy and distribution of the *Salix* species and hybrids found in Gower has been presented by the writer (Wilkinson, 1941 *b*), and attention has also been drawn to the cytogenetics of the Capreae group as represented in Gower (Wilkinson, 1944). The three Capreae species, namely, *S. caprea* L., *S. aurita* L. and *S. atrocinerea* Brot., are variously distributed, the variety *aquatica* of the last-named species being particularly abundant. Other *Salix* species, such as *S. repens* L., *S. fragilis* L. and *S. viminalis* L., also occur naturally in Gower, but with much less frequency and greater localization of distribution than the Capreae species. Of the naturally occurring hybrids, certain of these between the Capreae species are very prominent, as will be seen by referring to the accompanying map. Some colonies of *caprea* × *aurita* and *aurita* × *atrocinerea* are found, but the innumerable intergradations between *Salix caprea* and *S. atrocinerea* var. *aquatica* are particularly widely represented. It is of passing interest to note that Buxton (1934) similarly found a wide distribution and relative abundance of *S. atrocinerea* in the western part of the Isle of Wight, an area similar in certain respects, e.g. physical features and climate, to Gower.

Of the three Capreae species in question, *S. aurita* is the most restricted in distribution, and grows in damp and relatively high (250–300 ft.), exposed situations, such as that expanse of Fairwood Common lying due north of the Ilston Valley. *S. caprea* is more widely distributed, and typically favours relatively dry and upland situations (150–200 ft.) in the upper reaches of the valleys. *S. atrocinerea* is very much more abundant than the other two, and specimens can be found in almost any low-lying damp situation.

S. aurita and *S. caprea* hybridize, and typical segregates may be found on the southern fringe of Fairwood Common. The fact that these two species favour higher altitudes whilst *S. atrocinerea* occurs at lower levels does not militate against the incidence of

hybridity between *atrocinerea* and the other two species, for, as already pointed out, the topography of Gower is such that high and low situations tend to occur close together. Thus, small groups of *aurita* × *atrocinerea* occur at Fairwood and near Waunarlwydd; and several thickets composed of hybrids which exhibit many taxonomic intergradations between *S. caprea* and *S. atrocinerea* dominate the vegetation in certain situations in the upper reaches of many of the valleys, particularly on the southern side of the peninsula, such as Mayals, Killay, Newton and Oxwich. In addition to these rather circumscribed colonies, individual specimens of hybrid segregates from the *caprea* × *atrocinerea* range, particularly those approaching the *atrocinerea* parent in taxonomic characters, occur widely in many of the hedgerows in Gower.

As recorded elsewhere (Wilkinson, 1944), *S. aurita* and *S. caprea* are represented in Gower by both the diploid and tetraploid 'cytotypes' (to adopt the nomenclature advocated by the Council of the British Ecological Society), the basic chromosome number being 19. The tetraploid cytotypes are, however, by far the more frequently encountered. No taxonomic differences are apparent between the cytotypes of these respective species. All the *S. atrocinerea* material from Gower hitherto examined from the cytological point of view has proved to be tetraploid on the characteristic 19-base; and all the considerable range of intergrading hybrid types which have been subjected to cytological examination by the writer have similarly proved to be tetraploid, with 76 somatic chromosomes. It has been shown that the prominent thickets of hybrids derived from these two parents are composed for the most part of some F_1 types (which exhibit taxonomic characters approximately intermediate between those of the parents, coupled with the cytogenetical phenomenon known as 'amphiplasty'), together with a blend of types derived from the interbreeding of these through succeeding generations. Thus it seems clear that there are no irregularities of chromosomal behaviour of such a nature as would preclude the perpetuation of the various possible segregates from these two parental species, provided that the necessary factors of environment favour the occurrence of these segregates.

Particular interest obviously centres around those environmental factors which may condition the distribution of the species and hybrids of the Capreae. In common with Salices generally, they are rather intolerant of shade, and in the Gower situations where they occur, there is little light restriction. They also require an abundant water supply; thus *S. aurita* and *S. atrocinerea* are found in very wet situations, whether at high or low altitude, though *S. caprea* favours higher and drier situations in Gower. The respective hybrid ranges between *S. aurita* and the other two species flourish in wet and poorly drained situations; the *caprea* × *atrocinerea* thickets, however, occur in situations which are, on the whole, well drained.

Measurement of soil pH, which has been extensively undertaken from spring to autumn on the principal sites where the species and hybrids are found, has given results which appear to be significant. The measurements were taken in the field, using the B.D.H. Capillator, and the results are therefore relative and not absolute. To take the species first, *S. aurita* is restricted to high, sodden, and acid situations in which the soil has been derived from 'hill wash', the typical range of pH being 4·1–4·8. In the case of *S. caprea*, which is more widely distributed but favours a variety of relatively drier situations approaching the plateau level, the pH value has been found to vary from 5·8 to 7·3. Typical situations for this species with high pH values are found in the higher cleared regions of the Bishopston Valley which, as already pointed out, is a 'dissolved' valley on limestone;

in similar situations from Ilston to Pennard; and on the higher and better drained sites in the vicinity of Burry Green, where the limestone rests upon the Old Red Sandstone, and the depressions, though waterlogged, tend to alkalinity. The third species, *S. atro-*. *cinerea*, is by far the most widely distributed, particularly its variety *aquatica*, and dominates the *Salix* flora in all the low-lying, wet situations in Gower having a *p*H value on the acid side of neutrality. The measured *p*H range for the species has been found to vary from 4·5 to 6·5. It is interesting to note that, according to Pearsall (1938) *S. 'cinerea'* (= *atrocinerea* Brot.) colonizes above *p*H 5·1 or 5·2, and in this author's records does not occur on soils with a *p*H less than 4·5. In Gower, typical acid sites for this species are found in the vicinity of the waterlogged depression at Oxwich Marsh, where the glacial drift rests upon an impervious foundation of Millstone Grit and drainage is restricted by sand-dunes, and, similarly, in various depressions between Cefn Bryn and the north coast of Gower. An instance of a waterlogged but distinctly alkaline depression where *S. atrocinerea* is conspicuously absent is found south of Burry Green.

In the case of the hybrids, *caprea × aurita* and *aurita × atrocinerea* are found only in the neighbourhood of the *S. aurita* localities, and thus flourish in high and acid situations with a *p*H range 4·2–5·0. A striking correlation with *p*H value is found, however, in the case of the *caprea × atrocinerea* range of hybrids, where they occur in the aforementioned circumscribed sites towards the valley heads; the *p*H of the surface soil on such sites is found to fluctuate narrowly about neutrality, the observed range of *p*H being 6·8–7·1. Comparison of the map showing the location of these colonies of hybrids with the appropriate ordnance maps of the Geological Survey of England and Wales (Drift: sheets 246 and 247) reveals that, with two exceptions, the sites in question are located precisely on the marginal zones where the drift, here represented by Boulder Clay (in contradistinction to sand and gravel), thins out upon the limestone. In these situations the contribution of calcareous material to the soil is apparently sufficient to maintain a state of approximate neutrality. The two sites noted as exceptions (Mayals and Killay) are also on the edge of Boulder Clay, and the small amount of calcareous material necessary for the maintenance of neutrality is probably received from the remnants of nearby limestone dumps which have been continually replenished for some years for the purpose of local road-making.

An interesting observation on the distribution of land snails and slugs on a small area adjacent to the Mayals site mentioned above has been reported by Quick (1943), and may have a certain bearing on the present problem. The site in question, which is only thirty yards square, is described as the most interesting in Gower, partly because an exceedingly rare exotic land nemertine (*Geonemertes dendyi*) lives there (Waterston & Quick, 1937), but also because no less than twenty-seven snail species, mostly represented by small numbers of specimens, occur in that small area. The average *p*H of the surface soil in this locality is approximately 7, subject to slight seasonal fluctuation. It thus seems obvious that, other things being equal, conditions of neutrality tend to favour the attempt of the various species in question to establish themselves. A similar state of affairs may well apply to the *caprea × atrocinerea* swarms found in like situations in Gower.

It has already mentioned that certain segregates from the *caprea × atrocinerea* range, tending towards the *atrocinerea* parent in their taxonomic characters, are widely distributed in Gower, usually occurring singly or in small groups in a wide variety of

situations. The pH range hitherto recorded for such segregates is 4·8–6·8, and it is interesting to compare this with the corresponding range in Gower of *S. caprea* (5·8–7·3) and *S. atrocinerea* (4·5–6·5).

Lastly, it may be considered appropriate at this point to consider, in relation to habitat, some observations on rooting characters which have been carried out on the Capreae species and hybrids. Whilst dealing in former studies (1941*a*, 1944) with a much wider range of Salices, the writer observed that different species vary markedly in their ability to develop roots from cuttings when placed under identical conditions in plain water. Some, e.g. *S. viminalis, S. gracilistyla* and *S. fragilis*, developed abundant root papillae upon the submerged portions of the stem after about three days, followed by crops of roots; certain others, e.g. *S. repens, S. pentandra* and *S. polaris*, developed but few root papillae after a relatively long period (2–3 weeks), and only very infrequently was this followed by the appearance of roots. Varying intermediate conditions between these extremes were noted for a great many other species. Further, regular aeration of the cultures had a definite effect in inducing or increasing root formation in some species after the root papillae had appeared (e.g. *S. pentandra*), but not in others (e.g. *S. magnifica* and *S. medemii*). An extension of these observations on the species and hybrids of the Capreae group has been carried out, using twenty vigorous young cuttings (collected at random during early summer from different specimens) of each of the three respective species, and also of three suitable segregates from each of the three respective hybrid ranges. For each type studied, two groups, each containing ten cuttings, were placed in water and kept in a shaded region of the laboratory. The environmental conditions were thus the same for all the specimens. Two complete sets of cultures of all the types to be studied having thus been obtained, one set was aerated daily and the other set left undisturbed except for careful maintenance of the water level. The respective numbers of (*a*) root papillae and (*b*) roots developing upon typical strips of submerged bark, 10 cm. long and 1 cm. wide were noted, and also the respective numbers of days required for their appearance. The comparative effects of aeration and non-aeration of the cultures were also noted.

The cuttings of *S. caprea* showed the greatest reluctance to root, developing some 2–8 papillae/10 sq.cm. in 6–10 days, and only occasionally would a root emerge from a root papilla in the absence of aeration of the culture. About half the papillae developed roots after 15–30 days in the aerated cultures. In *S. aurita*, 4–12 papillae/10 sq.cm. were developed in 4–8 days, and most of these produced roots within 14 days, aeration having little apparent effect. In *S. atrocinerea* papillae were densely developed (15–25 papillae/10 sq.cm.) within 2–5 days, and nearly all of these gave way to roots within 10 days, whether the cultures were aerated or not. Indeed, two or three roots emerged together from some of the papillae. Moreover, in this species a new set of root papillae appeared after 3 weeks, duly succeeded by a fresh crop of roots. In the hybrids between *S. caprea* and the other two respective species, the rooting characters tended to resemble those of the parental species which rooted the more easily; thus, for example, cuttings of a *caprea × atrocinerea* hybrid, with taxonomic characters approximately intermediate between those of the parents, developed some 12–20 root papillae/10 sq.cm. in 3–5 days, and about two-thirds of these subsequently developed roots. A further extension of these observations to a much wider range of intergrades (twelve distinct types) has confirmed this conclusion.

The inherent ability to produce roots quickly and abundantly in waterlogged and relatively stagnant situations doubtless explains the rapidity with which *S. atrocinerea* can establish itself in such surroundings, whether multiplication of individuals occurs by vegetative means (e.g. suckers) or from seeds. To a somewhat diminished extent, this also applies to *S. aurita*. The characteristic occurrence of *S. caprea* specimens in small numbers, and the practical restriction of this species to well-drained upland situations, may well be correlated with its relative inability to root easily. All the possible Capreae hybrids obviously have one parent which roots fairly easily, and since the factors concerned with rapid and copious root production appear to express themselves in the hybrid progeny, the hybrids, generally speaking, have a much better chance of survival and of rapid multiplication than is the case with *S. caprea*; and in view of the fact that the non-endospermic seeds of *Salix* must germinate within a few hours of their liberation if they are to establish themselves, it is obvious that rooting characteristics in this genus have a considerable ecological importance.

It is interesting to consider these results in the light of Pearsall's observations (1938) on the occurrence of *S. atrocinerea* in typical successions on damp woodland soils. The willow successions appear to progress towards a zone on the borderline between oxidizing and reducing soils and become dominant on soils which are waterlogged and reducing for most of the year. The data obtained for *S. atrocinerea* in Gower lend further support to this conclusion, which can also be broadly applied to *S. aurita*. As already noted, these two Capreae species root readily in water, whether aerated or not. *S. caprea*, on the other hand, develops roots in water only with the greatest difficulty in the absence of aeration, and this is obviously correlated with the marked preference of this species for higher and better aerated situations in which the soils would tend to be of the oxidizing type. Thus, two different sets of habitat factors operate in determining the distribution of the Capreae species.

The detailed and extensive study in the field of the rooting habits of mature specimens of the Capreae presents a great deal of mechanical difficulty, partly because of the size of the root systems, but chiefly because these organs form a closed community. Examination of such specimens as have been accessible has shown that, as might be expected, *S. caprea* develops a relatively deep and not particularly extensive root system in the well-aerated sites where it flourishes, whilst *S. aurita* and *S. atrocinerea* develop comparatively shallow and widely spreading root systems in their normally damp respective habitats. On the whole, the hybrids appear to develop more vigorous root systems than the parental species, and, in the case of the *caprea × atrocinerea* range of hybrids, especially where the substratum is fairly well drained, the rooting habit has a tendency to resemble that of the *caprea* parent.

SUMMARY

In this paper an account is given of the distribution in Gower of the Capreae group of *Salix*, comprising the three species *S. caprea*, *S. aurita* and *S. atrocinerea*, and the naturally occurring hybrids between them. The effects of the physical features and the geology of the area, especially as these affect soil production, are discussed, and they are shown to be particularly important in connexion with the occurrence of the *caprea × atrocinerea* complex. The adaptational value of rooting characteristics is also noted,

especially in relation to the habitat factors which condition the segregation of *S. caprea* from the other two species.

The writer is particularly indebted to Prof. F. A. Mockeridge for advice and departmental facilities; to Dr M. Reese for advice on ecological matters; and to Prof. T. N. George and Mr Alan Stuart for suggestions and guidance on the geology of the area.

REFERENCES

Buxton, L. H. D. (1934). *J. Ecol.* **22**, 304.
Council of the British Ecological Society (1943). *J. Ecol.* **31**, 93.
Pearsall, W. H. (1938). *J. Ecol.* **26**, 194.
Quick, H. E. (1943). *J. Conch.* **22**, 4.
Waterston, A. R. & Quick, H. E. (1937). *Proc. Roy. Soc. Edinb.* **57**, 379.
Wilkinson, J. (1941*a*). *Ann. Bot., Lond.*, n.s. **5**, 149.
Wilkinson, J. (1941*b*). *Proc. Swansea Sci. Fld Nat. Soc.* **2**, 133.
Wilkinson, J. (1944). *Ann. Bot., Lond.*, n.s. **8**, 269.

A PRELIMINARY INVESTIGATION OF THE AVAILABILITY TO PLANTS OF THE WATER IN CHALK

By G. H. LOCKET

(*With four Figures in the Text*)

During the course of observations of the colonization of bare chalk at Harefield, Middlesex (Locket, 1946), it became clear that the rate at which plants could obtain water was an especially important factor. The problem can be approached by noting the nature of the root systems of the plants and also by measuring the water contents of the soil after subjection to known suction pressure.

In the first place it was found that the water content of well-drained chalk showed a remarkable steadiness (Tables 1 and 2), although plants growing on it may suffer from drought.

Table 1. *Water contents of specimens from a steeply sloping ridge of bare chalk in the Harefield pit*

Date	Depth in.	Water (percentage of dry weight)	Depth in.	Water (percentage of dry weight)
1934: 12 June	1½	20·7	7	21·2
19 July	1½	22·8	8–9	21·3
27 Sept.	1½	24·8	4–9	24·8
1935: 15 June	1½	30·5	12	28·2
10 Oct.	1½	24·4	12	27·7
1937: 2 March	1½	26·6		
25 May	1½	25·2	—	—
15 June	1½	24·0	6–8	22·4
20 July	1½	23·6	6–8	23·6
1938: 15 April	1½	23·3	8–9	21·8
17 May	1½	19·2	8–9	22·1

Thus measurement of water content alone is clearly not informative unless one knows how much of the water is available to plants, and in this connexion the state of subdivision of the chalk is important. In the ten years covered by the investigation, weathering of the chalk in a chemical sense cannot be a serious factor, as the following analyses of pure chalk and of specimens from a depth of 1½ in. at the same place on the floor at the Harefield pit show:

	Insoluble in 10% HCl in the cold %	Precipitated by NH₄OH from HCl solution %	CaCO₃ %	Total
Pure chalk	1·07	0·2	98·6	99·9
1½ in., 1935	3·2	0·3	97·2	100·7
1½ in., 1943	5·6	0·6	93·3	99·5

On the other hand, the physical effect of frost was very marked but difficult to measure since the finer particles are soon washed away into crevices.

The effect of pulverization on the water-holding capacity of chalk was explored as follows. Three samples of chalk (taken from the same block)—consisting of (a) solid chalk (whittled down to make flat pieces 3–4 mm. thick), (b) powder passing a 1 mm. but retained by a 90-mesh sieve and, finally, (c) a very fine powder,* obtained by elutriating chalk ground under water—were all subjected to varying suctions up to a pressure of 1 atm. by placing them on filters of sintered glass or on unglazed pot, covered with a very thin layer of the 'fine-silt' fraction of an ordinary garden loam and fixed into a funnel with pitch. With solid samples contact with the filter was made through powdered chalk.

The apparatus was essentially that of Haines (1930); under suction water, but not air, could pass the filters. For pressures above 200 cm. of water, the filters were fixed in Buchner funnels connected to a filter pump and mercury manometer, and they were always covered with a tin, lined with wet blotting paper, to prevent loss of water by evaporation (Fig. 1). With chalk, equilibrium was established in a few hours, but all measurements were made when a constant suction had been applied for 24 hr. Higher values than 1 atm. for the suction pressure were obtained for the powdered samples, from freezing-point measurements, using a slight modification of method 'B' of Schofield & da Costa (1938).

The curves (Fig. 2a) show the water content of chalk, previously left under water, plotted against the applied suction pressure, which is measured in Schofield's logarithmic pF scale. (Thus pF 1 = 10 cm., pF 2 = 100 cm., pF 3 = 1000 cm. of water and so on.) They thus show the behaviour of chalk being dried progressively; a different curve would be obtained for dry chalk taking up water, but this is not so relevant.
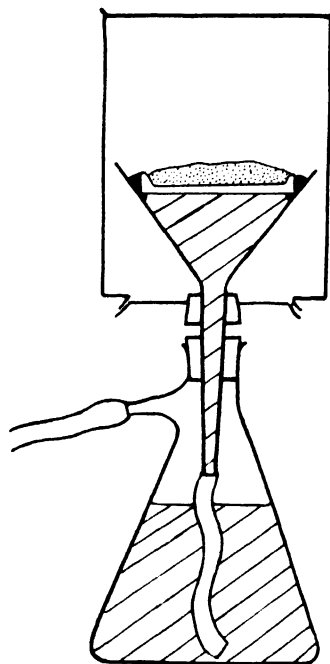
Fig. 1.

These curves reveal the following facts. First, solid chalk loses practically no water up to a suction of pF 3·0 (about 1 atm.). Such water as it contains will therefore not be readily available below this suction pressure, which accounts in large measure for the steady water content of chalk over dry periods. This result is amply borne out by measurements on samples of chalk from other regions (see Fig. 2b, c and d).

In contrast to the behaviour of the solid, the sieved powder suddenly loses more than half its water at a suction of about 10 cm. of water (a value which presumably depends on particle size) and then approximates in behaviour to the solid. The elutriated powder has a much smaller water-holding capacity under free drainage, but loses water more steadily as the suction is increased. The freezing-point measurements give a wilting point corresponding to some 4–5% of water on the different chalks (W4 containing 76% of chalk gave a value of about 10%). All water present in greater quantity must be available to some extent.

Possibly of equal or of more ecological importance than the wilting coefficient is another quantity, less easy to define and probably varying amongst plant species, and that is the suction pressure against which a plant just fails to 'flourish', by which I mean that it

* The size of the particles in this elutriated powder ranged from $2 \cdot 8 \times 10^{-2}$ to $7 \cdot 5 \times 10^{-4}$ mm., the majority being about $2 \cdot 8 \times 10^{-3}$ mm.
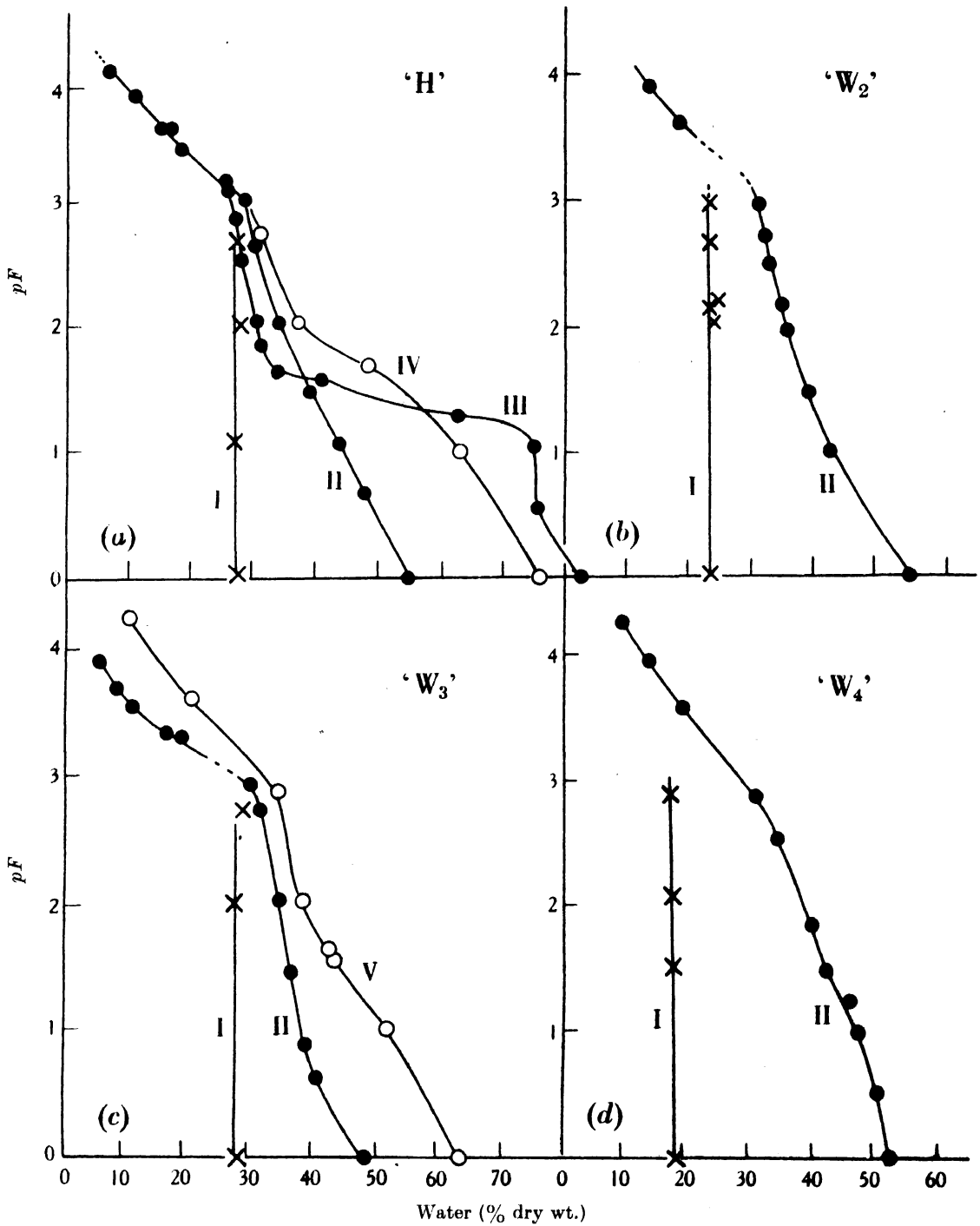
Fig. 2. The variation of water content with suction pressure during the drying of chalk from different localities. I, solid chalk; II, elutriated powder; III, particles passing a 1 mm. and retained by a 90-mesh sieve; IV, soil from roots of *Festuca* (H); V, overlying 'organic' layer (W 3).

just fails to exert its full influence as a competitor, as far as its vegetative growth is concerned, in the community. It may not be possible to define such a point accurately, but the following observations show that some degree of comparison is possible and that for a given species it should be possible to find a pF value indicating drought conditions in a particular soil, especially if root development is fairly uniform, as is the case here. In the first place soil was taken from the roots of *Festuca*, which was dying back owing to drought, and the field water content measured. The rest of the sample was passed through a 2 mm. sieve and, after soaking for 24 hr., was subjected to varying suction pressures. The curve is shown in Fig. 2*a*, from which it is seen that the field water content, 30·7 %, corresponds to a pF of about 2·7. Water held more firmly than this will not readily be available in conditions of evaporation obtaining during a drought in this locality. In order to get some sort of check on this result a laboratory experiment was carried out on *Lotus corniculatus*, a seedling of which was grown in chalk powder in a cavity 1 in. diam. and 1½ in. deep in a large block of chalk lying in water. Buried in this block was a glass tube plugged at the end with fired clay and surrounded with puddled unfired London clay, the hole being filled in and covered with cement. This tube was filled with water and connected to a suitable mercury manometer and the water round the chalk allowed slowly to evaporate. As was to be expected the pressure began to rise rapidly as soon as the chalk started to dry out and was recorded whenever the plant began to wilt.

Date	Rel. hum. (wet and dry bulb)	Suction pressure at which wilting began cm. Hg	pF
1943: 6 July	—	45	2·8
17 October	—	39	2·7
1–4 December	50 %	45–49	2·8
1944: 26–29 February	50 %	47–51	2·8

The values for the pF when the plant received a definite set-back and began to wilt (2·7–2·8 approx.) are thus not very different from that for *Festuca* obtained in the field. Thus it does appear that drought conditions will be recognizable, in a chalk soil at any rate, if the value for pF rises to much above 2·7 in the summer months, and the figures in Table 1 indicate that the slopes at Harefield are subject to drought in spite of the steady water content.

During 1938 another investigation was carried out by taking water contents of specimens from chalk and from an 'organic' layer above it. The site (W 3) was on a low hillock, an outlier of the Chiltern ridge (where sand or soil washed down from above could not occur) close to Whiteleaf, Prince's Risborough. The ground had last been in cultivation about 1924 and was sparsely though fairly uniformly covered by a typical chalk flora, rather severely cropped by rabbits. A survey of the top layers on lines suggested by Dr Graham Brade-Birks revealed three main horizons:

(1) To about 2½ in. A typical brown-grey organic layer (it would be possible to divide this layer into two with some difficulty, but this has not been attempted here).

(2) 2½–4 to 6 in. A layer containing lumps of chalk up to about ½ in. diam. mixed with soil typical of (1).

(3) 6 in. downwards. Chalk rock fissured into blocks about 6 in. square by 2 in. The interstices were very fine but often contained the remains of dead roots, which only very rarely penetrated the solid chalk. For present purposes a comparison was made between (1) and (3) and the results are shown in Fig. 3.

Table 2. *Water contents (percentage dry weight) for chalk and overlying organic layer (W3) (1938)*

Depth	Jan.	Feb.	Apr.	June	July	Oct.	Nov.	Jan. (1939)
2½ in.	37·9	30·4	21·1	22·1	20·9	29·4	31·1	36·2
	(2·1)	(2·7)	(3·4)	(3·3)	(3·4)	(2·9)	(2·6)	(2·2)
7–9 in.	28·7	29·0	22·8	21·8	21·2	27·9	28·5	28·6
				(3·3)	(3·3)			
Dates of collecting	10th	20th	19th	12th	22nd	6th	27th	15th
R1 (in.)	3·17	0·41	0·13	0·41	0·83	2·61	2·54	– –
R2 (in.)	—	0·16	—	0·30	0·23	0·22	2·59	1·93

R1 = monthly rainfall at Princes' Risborough (Air Ministry).
R2 = rainfall during the 10 days before samples were collected at Whiteleaf.
pF values are in brackets.
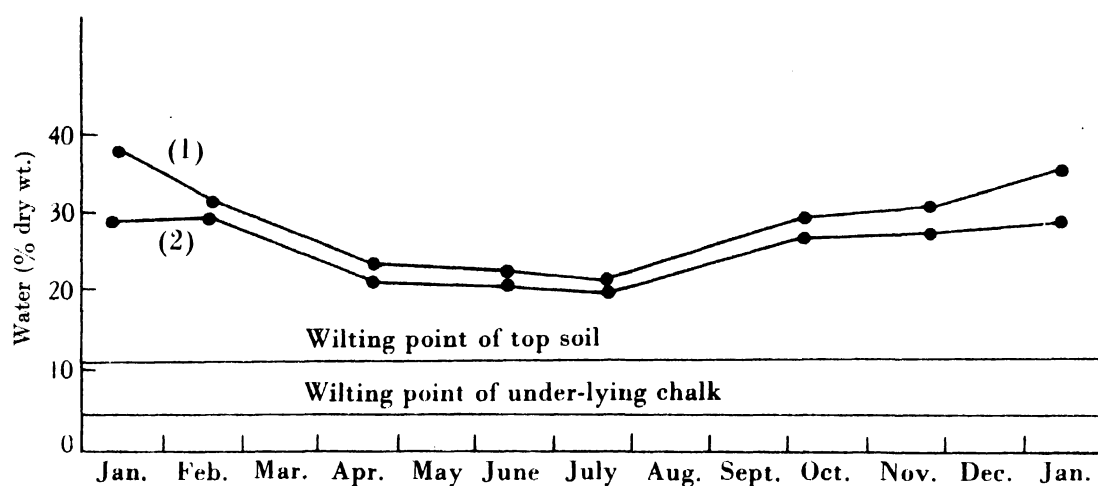
Fig. 3. Water contents of top soil and of underlying chalk (1938) (Whiteleaf, W3).

It will be seen that during the wet season the organic layer contains substantially more water, but for the dry summer the values nearly coincide. The results are similar in general to those of Anderson (1927), although she was dealing with a much thicker, more mature, organic layer. In the present case it is interesting that the same general effect should be produced with such a small increase in the organic and clay-sand content over that of chalk (see analyses, p. 227). In order, however, that these results should be significant the wilting coefficients for the two lots of soil were obtained by freezing-point measurements which gave 11 % for the top layer and 4 % for the underlying chalk. This had, of course, been pulverized by the borer, but the value for the wilting coefficient is not likely to be much affected. Subtracting these values from the percentages of water actually found should give a measure of the water available to plants. Actually, the number so obtained is greater for chalk than for the overlying organic layer, except in the wettest season, and, since above *pF* 3 the water content-*pF* curves run nearly parallel, there must be more available water in the chalk.

Further, by interpolating these water contents on *pF* curves obtained by subjecting the soils to suction in the laboratory (Fig. 2c), one may get a value for the *pF* during the time in question. The results are shown in Table 2. (Owing to the nature of the *pF* curve it is not possible to find *pF* values for chalk below 3·0 (1 atm.), but in June and July the

figures agree closely with those from the top layer and indicate that both layers on this well-drained site were suceptible to drought.)

Analysis of chalk from different sites investigated

Site	Insoluble in cold 10% HCl %	Precipitated by ammonia from HCl solution %	CaCO₃ %	Organic %	Total
H (Harefield)	5·8	0·6	93·2	—	99·6
W2 (chalk pit at Whiteleaf)	8·0	0·7	90·8	—	99·5
W3 (chalk below organic layer, Whiteleaf)	1·4	0·3	99·0	—	100·7
W3 (organic layer)	3·0	4·7	88·2	3·4	99·3
W4 (site of suction measurements, Whiteleaf)	22·2	0·7	76·1	—	99·0

Since pF values below 3 for chalk cannot be measured by taking water contents, an independent field experiment was carried out at a nearby site (W 4) where the chalk, although getting near the underlying greensand and containing some 22% of insoluble matter, yet
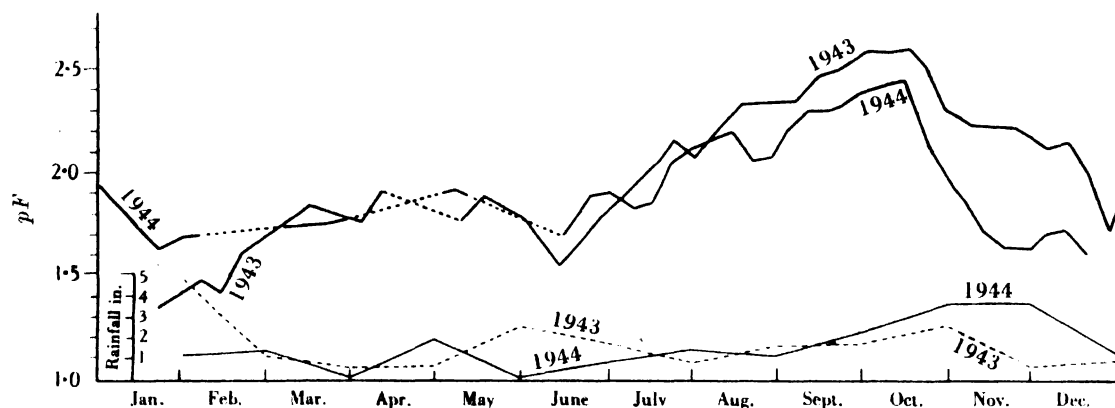
Fig. 4. Variation of suction pressure in chalk measured in the field (Whiteleaf, W 4) in 1943 and 1944. Monthly rainfall is shown below.

behaved typically under suction (see Fig. 2d). The apparatus was essentially the same as that used for the laboratory experiment and described above, a lump of well-puddled clay being found to be the most satisfactory material for allowing the passage of water without air. The apparatus was in a covered pit, some 2 ft. deep, to avoid damage by frost, the bottom of the suction tube being 3½ ft. below the surface of the soil. The bore-hole by which the tube entered was 18 in. deep, the clay plug and tube being cemented in.

The figures given for the years 1943 and 1944 are shown in Fig. 4. and it is interesting that the suction reaches a maximum in the October of these years of low rainfall. The curve showing the level of water in a tank subjected to rainfall, evaporation and 'drainage' (represented by uniform regular withdrawals) shows a minimum at just about the same time (Bilham, 1938).

It was noted very early on in the period covered by the chalk-pit observations that there was a tendency for the root systems of plants to exploit the upper 2 in. of weathered soil. This was especially striking in the case of *Betula* and *Salix*, and specimens of *Cirsium lanceolatum* and *Artemisia vulgaris* were found to be thriving with their long

tap roots running horizontally. *Daucus carota*, which sent a deep tap root into some cinder banks, developed a shorter more diffuse root system when growing in the top 2 in. of weathered chalk. The most important early colonizers (with the notable exception of *Lotus* and *Melilotus*) seem to depend on the existence of this weathered layer; moreover, they tend to be susceptible to drought, although the water content of the underlying chalk remains so steady. From what has been said above this is no longer surprising, since, for a pF above about 2·7, it seems probable that a plant cannot maintain itself with vigour, and little water will be available from solid chalk until the pF reaches a value of 3. (It is worth noting, however, that if solid chalk lies between a reservoir of water and a plant's roots, there is no reason to suppose that it cannot pass water on from a region of high to low vapour pressure.) It is very doubtful therefore whether, on well-drained chalk, the steady reserve in the solid is of value to the plants in resisting drought, except that it does enable them to keep alive, for the water available between pF 3 and 4·2 (the wilting point) is considerable. During vigorous growth the roots will tend to find the readiest water supply which lies in the weathered material. The deeper rooting plants exploit fissures in the chalk, though only one, *Cirsium arvense*, was found to have bored through the solid rock (Whiteleaf, site W 3). These fissures usually contain powdered material, and, as is well known, water in chalk moves through these primarily and not through the solid rock. In extreme drought those plants (e.g. *Lotus* and some *Salix* and *Betula*) which have extensive root systems in contact with the solid will be able to draw water from it at a pF greater than 3 and so keep alive.

The following list shows the behaviour of the roots of a number of plants colonizing bare chalk at Harefield.

u. = exploits the upper weathered region (usually about 2 in. deep).
l. = penetrates deeper, exploiting fissures in the rock for the most part.
If both symbols are used, the first denotes the plant's preference.

Acer pseodoplatanus	l.	
Achillea millefolium	u.	
Agrostis stolonifera	u.	
Arrhenatherum elatius	u.	Tends to go deeper into crevices and exploits top of solid chalk
Artemisia vulgaris	u.	Tending to run some distance
Betula alba	(on floor)	Runs under the surface with scarcely any penetration. Length of main roots equals height of tree (roughly)
	(on slopes)	Movement of chalk tended to leave roots bare, but here they follow the crevices down
Cirsium arvense	l.	Goes straight down (seen to bore solid chalk at Whiteleaf)
C. lanceolatum	l.	But may run horizontally u.
Centaurea nigra	u., l.	
Chrysanthemum leucanthemum	u., l.	
Clematis vitalba	l., u.	
Crataegus oxycantha	l.	
Crepis biennis	u., l.	
C. taraxacifolia	l., u.	
Dactylis glomerata	u.	But on loose chalk boulders penetrates deeply
Daucus carota	l., u.	
Epilobium angustifolium	l.	Runners explore upper region, but roots go down crevices
Festuca rubra/ovina	u.	
Fragaria vesca	u.	
Fraxinus excelsior	u., l.	
Hieracium pilosella	u. (some go deeper)	
Hypericum perforatum	l. (goes deep), u.	
Leontodon hispidus	u.	
Linaria minor	u.	
Linum catharticum	u.	
Lotus corniculatus	l. (u. only a little—cf. Medicago lupulina)	
Medicago lupulina	u., l.	
Melilotus officinalis		

Orchis maculata	l.	
Origanum vulgare	u.	
Plantago media	u.	
Potentilla reptans	l.	Deep penetration
Quercus robur	l.	
Ranunculus bulbosus	u.	
Reseda lateola	l.	
Rubus fructicosus	l. (u.)	
Rumex acetosa	u., l.	
Salix caprea/cinerea		Like Betula
Scrophularia nodosa	u., l.	
Senecio crucifolia	l., u.	
Sonchus oleraceus	u., l.	
Taraxacum officinale	l.	
Tussilago farfara		Runs along, some roots go down
Veronica chamaedrys	u.	
Vicia sativa	u.	

CONCLUSIONS

1. The water in pulverized chalk is much more readily available to plants up to a suction pressure of 1 atm. than that in the solid (which parts with very little water up to this pressure). Some species adapt their root systems on chalk to exploit this more available water.

2. Drought conditions prevail in chalk when the suction pressure is about pF 2·7–2·8 (500–600 cm. of water). The large amount of water available between pF 3·0 (1 atm.) and 4·2 (the wilting point) may well keep alive those plants which are able to exploit it, but they cannot 'flourish' on it, in the sense of increasing vegetatively.

3. Direct measurement in the field 3½ ft. below the surface revealed something approaching drought conditions in chalk in October 1943.

REFERENCES

Anderson, Violet L. (1927). Studies of the vegetation of the English Chalk. V. *J. Ecol.* **15**, 72.

Bilham, E. G. (1938). *The Climate of the British Isles.* p. 126. London.

Haines, W. B. (1930). *J. Agric. Sci.* **20**, 97–116.

Locket, G. H. (1946). Observations on the colonization of bare chalk. *J. Ecol.* **33**, 205.

Schofield, R. K. & da Costa, J. V. B. (1938). Measurement of pF in soil by freezing point. *J. Agric. Sci.* **28**, 644.

THE DISTRIBUTION AND STATUS OF *GLYCERIA MAXIMA* (HARTM.) HOLMB. IN THE REGION OF SURLINGHAM AND ROCKLAND BROADS, NORFOLK

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(*With Plates* 11 *and* 12 *and eleven Figures in the Text*)

CONTENTS

A. INTRODUCTION AND METHOD OF PROCEDURE

It is now over 30 years since the fen communities of the Yare Valley were first described by Pallis (1911), and since then little fresh ecological work on this region was attempted until a paper by Ellis (1934) on the Wheatfen area north of Rockland Broad gave fresh stimulus to further investigation. This present paper represents an attempt to throw further light upon the interrelationships of the reedswamp and fen communities in the region of Rockland and Surlingham Broads and especially to establish the part played by *Glyceria maxima* in the general facies of the vegetation. It incorporates the results of field observations made intermittently since 1939, culminating in a more detailed survey of the whole region carried out during August and September 1944.*

The results of the survey are partly embodied in the accompanying folding map (Fig. 1). Here, only the position of *G. maxima* itself is shown for the fen regions, although the extent of carr and woodland over the area is also indicated. The general distribution of the other dominant species is largely covered by the text description.

The mapping of the communities was carried out with the aid of outline tracings made from 25 in. Ordnance Survey Maps (1928 edition). The limits of these communities were plotted mainly by eye and by means of rough paced measurements. It was found that the presence of very numerous dykes over the major part of the area was invaluable in providing a guide to the positions of the various communities by giving a framework within which the area could be divided up on a sectional basis. Very few new dykes have been cut since the last Ordnance Survey, but some of those shown in the 1928 map are now completely blocked and overgrown, and are now only distinguishable by a slight depression in the fen surface.

Accompanying the main map (Fig. 1) is a small inset map giving a numerical key to the chief areas subsequently referred to in the text, this being thought simpler than a reference to the areas by their local names. In the case of the Wheatfen area,* however, where much of the preliminary work was carried out and where frequent reference is made to smaller units than those covered by the numerical notation, a separate diagram is given (Fig. 2), based on the map published by Ellis (1934). The information given in Ellis's original map was largely used in the plotting of the communities of areas 30–32 and 36–38.

Fig. 2. Sketch map to show the main waterways at Wheatfen. Based on the map published by Ellis (1934).

It was not found possible in the time available to survey the whole of the area in the same detail. Areas 47–51 were not visited at all, and areas 1–3 and 52–54 were only examined superficially. These are shown on the folding map by cross-hatching.

* The name 'Wheatfen' is subsequently employed in referring in general to the estate, some 150 acres in extent, surrounding the major part of the chain of waterways leading from Rockland Broad, and of which the 'home' water of Wheatfen Broad forms part. This estate is shown on the inset map by stippling, and it was owned by the late Mr J. D. Cockle, whose ready co-operation and provision of facilities were much appreciated.

B. GENERAL DESCRIPTION OF THE AREA SURVEYED

The area under consideration is situated on a strip of fen peat of varying thickness running parallel with and occupying a loop of the main river. Its relationship with the peat basin as a whole can be traced out in the map published by Pallis (1911, p. 217). A number of diggings made during the course of the survey showed that the thinning out of the peat at the westward edge of the basin corresponded very approximately with the eastward boundary of pasture and cultivated land, as indicated on the folding map. At this boundary the peat abuts upon River Gravel throughout the greater length of the basin, though in the region of Rockland Broad and the southern part of Wheatfen it is bounded by both clay and pebbly sand of the Norwich Crag. The underlying gravel pan in some places approaches the surface within the peat basin itself to form local 'hard-bottom islands', as in parts of Wheatfen (Ellis, 1934).

The peat has been formed by the gradual filling up of originally large open water areas, of which the present small expanses of Rockland and Surlingham Broads, and the still smaller open water areas linked with these, form the few existing remnants on the west side of the river. Similar areas occur across the river especially in the region of the almost obliterated Strumpshaw Broad, but although these provided some useful evidence in working out the main hypotheses put forward in this paper, they were not surveyed in detail and are therefore not incorporated in the map.

It is supposed that Rockland and Surlingham Broads originally formed part of a single large open water expanse, and surface contours suggest that the region at which they first became separated lies somewhere in the vicinity of the lane leading down to the Coldham Hall Ferry. The open water of these Broads was apparently completely cut off at first from that of the main river, but at some stage in their history artificial connexion was made between the Broads and the river by means of dykes cut through the intervening peat and alluvium.

The open water of the river and interconnected Broads and dykes of the region is strongly tidal, with an average fluctuation of some 20–30 cm., but with a far greater maximum range augmented still more by exceptional meteorological conditions. It has been suggested[*] that the opening of the much wider New Bridge at Yarmouth in 1930, to replace the old 'bottle-neck' bridge, has had the effect of allowing greater upflow of water on the incoming tide of the Yare; this may explain the generally observed fact that winter flooding by master tides has recently become more frequent and severe. The tidal water is not normally brackish at this distance from the sea, although exceptional tides may cause some increase in salinity. Ellis (1934) gives a normal chloride content of $0.1\,^0/_{00}$ for the water of the Wheatfen region, though during exceptionally high tides in January 1943, a value of $1.1\,^0/_{00}$ was recorded for Wheatfen Broad (Ellis, 1943, unpublished).

The connexion between the Broads and the tidal river results in a continual circulation of water throughout the whole system (thus contrasting strongly with the Broads of the other East Norfolk rivers, especially those of the Bure, cf. Pallis (1911, p. 225)). The direction in which the filling-up process of the Rockland and Surlingham basins is now proceeding is in line with the downflow current of the main river, as might be expected from mechanical considerations, and the largest open water areas are situated towards

[*] Personal communication from Mr K. E. Cotton of East Norfolk Rivers Catchment Board.

the lower (seaward) ends of the two systems of residual open water. Whereas Rockland Broad is in communication with the main river on one side only by comparatively long dykes, the main open water area in the Surlingham region is connected with the river by much shorter dykes on two sides, so that there is a very free passage of water across it. Moreover, this water flow is further assured by the position of the latter Broad in relation to the loop of the river, since a considerable proportion of the water travelling along the river channel is short-circuited across the base of the loop via the Broad.

Parts of the banks of the river itself, and of the main navigable dykes between the river and the Broads, are raised to varying heights by deposited dredgings. As may be seen from the map, these embankments frequently bear a line or band of trees, with *Salix alba* L. and *S. viminalis* L. prominent; the banks are however broken through at frequent intervals by dykes running back through the peat at right angles to the river. Differences in the drainage conditions over various parts of the area were found to be of prime importance in determining the detail of the distribution of specific plants, and will therefore be analysed more fully later.

In its upper reaches above the Surlingham area, the Yare passes for a considerable part of its course through strata of the Upper Chalk, and hence the open water is slightly alkaline in reaction. A series of colorimetric pH determinations made at various points in the open water systems since 1939 have given a constant value of 7·2–7·3. Similar preliminary field tests on soil samples taken over the area have shown that, on the whole, the substrate is circum-neutral with a pH range of from 6·2 to 7·3, but with most values in the latter region.

With regard to the anthropogenic factors of the habitat, it could be clearly seen that the plant communities of the area could be placed in two well-marked groups:

(1) The communities of the primary succession from open water, developed in regions where peat is still being actively formed, and where human interference is at a minimum. Here the substrate is relatively soft and unconsolidated. These communities occupy the following areas:

Surlingham Broad region: Parts of areas 1–6; western outliers of area 7, beyond the embankment; most of area 8.

Rockland Broad region: Parts of areas 37, 41, 46, and to a lesser extent 52.

(2) The secondary anthropogenic fen communities occupying mainly the intermediate areas between the two Broads. These areas would normally be covered by carr and woodland, but in most cases they have been maintained as fen by cutting and clearing. Such cutting has been far more frequent in the past than at present, and some areas are now reverting to carr. The fen peat is here older, and consequently more compacted and consolidated than in (1) above.

These two types of communities, though somewhat similar floristically, are very different in origin, and will therefore be subjected to separate analysis in the subsequent pages.

C. THE COMMUNITIES OF THE PRIMARY SUCCESSION

(1) *Comparison of the general characteristics of the chief areas involved*

The extent to which the two residual water systems (at the Surlingham and Rockland ends of the peat basin respectively) have filled up during the last century is shown in
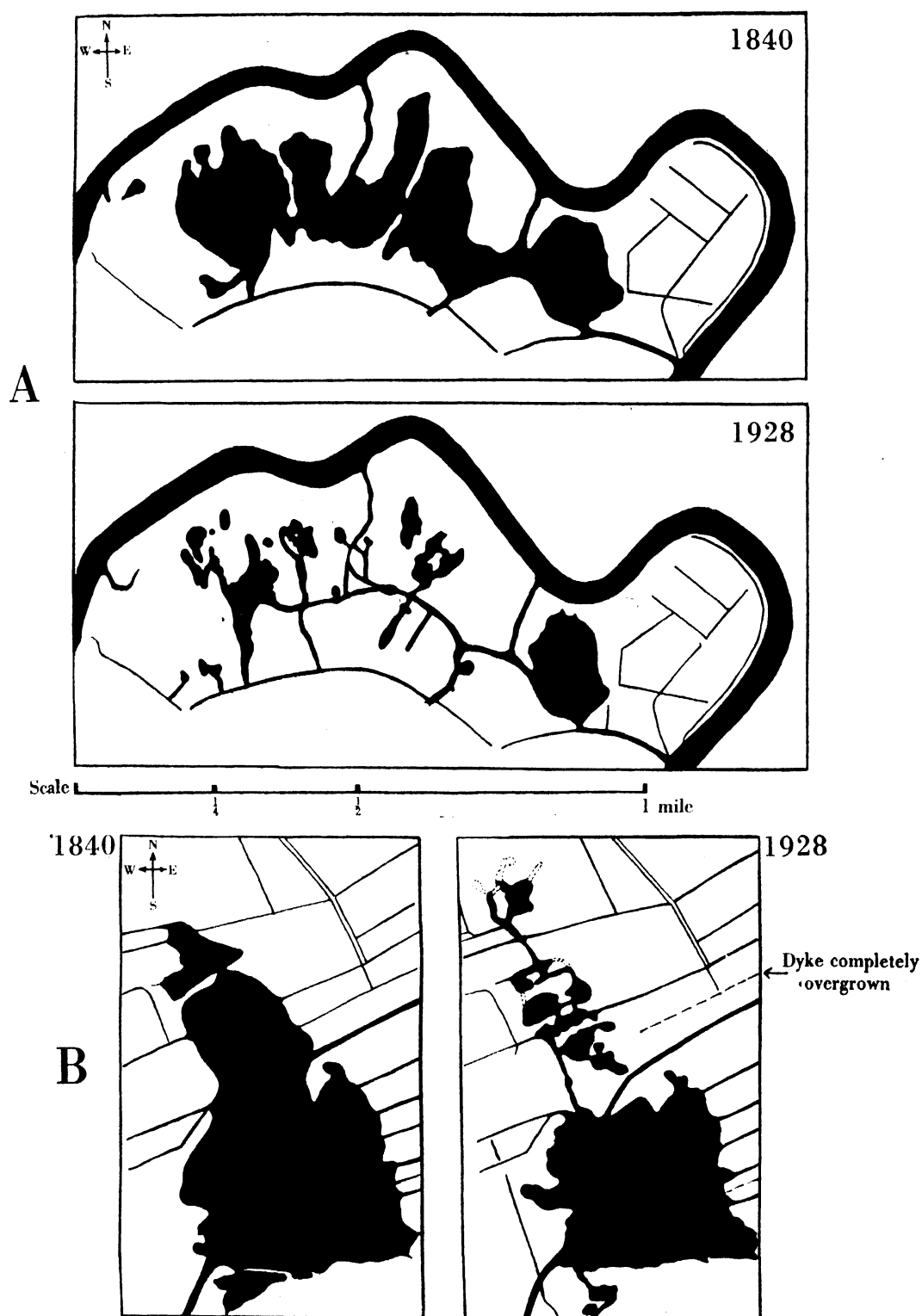
Fig. 3. Maps showing the decrease in the extent of the open water during the last century in (A) Surlingham Broad, and (B) Wheatfen and Rockland Broads. The earlier maps are reduced from copies of *Maps referred to in the apportionment of the Rent Charge in lieu of Tithes, 1840,* and the later maps are reduced from 25 in. Ordnance Survey Maps, 1928 edition.

Fig. 3.* The two systems differ in one important respect. In the Surlingham area the vegetation has been allowed to encroach on the open water more or less unchecked, apart from certain periodic clearing of the main channels to allow access by boat for reed-cutting and duck-shooting. In the Wheatfen chain of waterways, however, the open water areas have been maintained well beyond their natural existence by a far more intensive clearance of the encroaching vegetation, and in addition some new waterways have been opened up at the distal end of the chain. This artificial backward extension of the open water may be clearly seen by comparing the 1840 and 1928 maps in Fig. 3; some of the more recent of these new waterways are not included in the original 1928 Ordnance Survey Map, and these are shown in Fig. 3 by dotted lines. In addition, certain other channels, not shown in this figure, have more recently been opened up in the region of Avenue Pool. Hence, at Wheatfen, many of the intermediate stages in the primary succession have been lost or obliterated in parts, so that in many places carr abuts immediately upon open water. It was therefore found that an analysis of the relationships of the main communities in the Surlingham area was an essential preliminary to an understanding of the distribution of corresponding communities at Wheatfen. The simpler distribution of the vegetation in the former area will therefore be described first as forming a basis for the interpretation of that of the latter (though it is convenient in places to draw some specific illustrations from Wheatfen, and to make certain direct cross-comparisons where relevant).

The remaining open water at the Surlingham end of the peat basin now consists only of a narrow central tidal channel with small overgrown subsidiary arms, the former leading into the larger and more open eastward expanse which is all that is now generally included under the designation of 'Surlingham Broad'. (To avoid subsequent confusion in the use of the name, the whole of the original expanse will in future be referred to as 'the *old* Surlingham Broad', in contradistinction to 'the *present* Surlingham Broad' which refers only to the open water at the eastern end.) In addition to the artificially formed dykes connecting the present Surlingham Broad with the river, contact was also made in the past between the river and one of the subsidiary lateral arms of the old Broad. Moreover, the tidal dyke running to the south of areas 1, 2 and 4 has been artificially cut and maintained, and connexion has been made between this and certain other of the arms. As a result of these connexions, the majority of the remaining open water areas of the old Broad are, or have been, under direct tidal influence with a continual circulation of water. This circulation is now limited to some extent by partial overgrowth of the main channels in recent years, but nevertheless there is still considerable water movement within the system. The maps show, however, that a few isolated pools have for some time been completely separated off from the main system, and are therefore no longer tidally affected. It will be seen later that these areas have no especial significance in the interpretation of the community relationships.

The substrate of the Broads is a deep, oozy organic silt forming a layer several feet in

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* The 1840 Tithe maps which are used in this figure are regarded as far more accurate in showing the limits of the open water at that time than Ordnance maps of comparable date. In the case of the latter, little direct correspondence could be traced with the present outline of the water when the 1928 maps were superimposed upon them; but with a similar superimposition on the Tithe maps (reduced to the appropriate scale), the actual derivation of the present residual arms of open water from definite larger expanses could be clearly traced out.

thickness in some parts. Preliminary percentage loss on ignition determinations gave the following values for this basal ooze:

Deep Waters, Wheatfen $\qquad$ −19·35% ⎫ Both samples taken within upper 10 cm. of ooze,
The present Surlingham Broad $\quad$ −16·58% ⎭ from areas relatively sheltered from tidal scour.

The high organic nature of the silt is largely due to the annual autumnal decay of the dense masses of *Ceratophyllum demersum* L., which forms extensive mats floating just below the surface and chokes the Broads throughout the summer.

The ooze is especially soft and yielding in the larger open water areas, where the force of the tidal flow is expended over a greater surface and the finer particles of silt, scoured from the narrower channels, are deposited. In these areas, the upper layers of the ooze appear to be semi-suspended in the water and are disturbed by the slightest movement. It is thought that the lack of mechanical stability in these surface layers may be partly responsible for the absence of rooted submerged aquatics from many parts of the Broads, though the shading effect of the summer *Ceratophyllum* mat must also be very effective in limiting the distribution of such species.

(2) *The stages in the primary succession from reedswamp to carr*

(a) *The marginal reedswamp communities*

In that part of the Surlingham Broad region which was surveyed in detail, the reedswamp communities bordering the open water were found to be dominated almost entirely by *Phragmites communis* Trin. and *Glyceria maxima*. Other reedswamp species were either absent, or played a very subsidiary role, in those areas where *active primary colonization* of open tidal water was taking place, and which possessed the *typical loose basal ooze*. The significance of this point lies in the fact that observations made during the course of the primary survey suggested strongly that mechanical factors of the habitat play a very important role in determining the distribution of reedswamp species both at Surlingham and in the Wheatfen-Rockland area.

(i) *The relationship between* Glyceria *and* Phragmites *reedswamp.* The colonization of the open water of the old Surlingham Broad has been completely unchecked by any cutting or clearing whatever since 1939, and in those parts where *Glyceria maxima* reedswamp abutted directly upon open water it was found that the outer edge of the Glycerietum consisted of an entirely free-floating mat of intertwined rhizomes, roots, and trailing aerial shoots; farther back the interstices between the rhizomes and roots are filled up by water-borne silt and decaying *Glyceria* debris, so that the whole structure ultimately forms a comparatively solid raft possessing a considerable range of vertical movement in relation to tidal levels. This part of the Glycerietum is in future referred to as 'floating *Glyceria* reedswamp'.

The adoption of this floating habit by *Glyceria* (which in other habitats is normally anchored in the substrate) is here thought to be the direct result of the interaction of certain mechanical factors peculiar to the Yare Broads—namely, the fairly extensive diurnal tidal fluctuations in the water level *combined with* the great instability of the basal ooze. The normal rhizome system of *Glyceria* from other habitats with a more stable substrate was found to be of a superficial type, and to be mainly confined to the upper 10 cm. of such substrates. *Hence it is suggested that the constant recurrent lifting effect of*

a twice-daily rise of some 20–30 cm. in the water level, exerted constantly throughout the whole year (and especially effective in the summer when the development of semi-prostrate air-containing aerial shoots gives the maximum buoyancy) is sufficient to prevent the anchorage of the roots and rhizomes in the loose, easily disturbed layers of the basal ooze. The vegetative morphology of *Glyceria* is such that it is better adapted than most other reedswamp species to the maintenance of this floating habit under such mechanical conditions, and it is hoped to consider this point more fully in a later paper.

In contrast to *Glyceria, Phragmites* is able to maintain itself under the same conditions by an entirely different growth habit. The rhizome system of *Phragmites* is normally deeply situated; Pallis (1915, p. 248) maintains that for *Phragmites* in general the branching is mainly in the horizontal plane in shallow water, but that in deep water it branches vigorously in a vertical plane from a deeply situated horizontal parent rhizome. This type of growth often results in the formation of reed-stools by the accumulation of silt round the closely adpressed bases of the vertical shoots, and such reed-stools are typical of the *Phragmites* reedswamp of this area. The deep initial anchorage and the subsequent accumulation of silt to form the reed-stools give *Phragmites* a fairly stable basis even in the loose ooze of the Broads, and allows the erect development of the stiff vegetative and flowering shoots which, being upright, offer minimum purchase to the lifting water.

Whereas the *Phragmites* reedswamp thus anchored is mechanically stable except under abnormal conditions of scour, the floating *Glyceria* reedswamp is very liable to disintegration by purely physical forces, so that free-floating masses, known as 'hover', may very commonly be seen drifting up and down the main tidal waterways. Despite the fact that *Phragmites* reedswamp occurs abundantly within the region, it has been observed that by far the greatest number of free-floating masses of vegetation seen in the area consists of *Glyceria*, while a detached floating portion of *Phragmites* reedswamp is comparatively rarely seen. The relative ease of mechanical disintegration of the two types of reedswamp is well illustrated by the following observation. In 1939, a floating *Glyceria* reedswamp of the type described was seen to be developing side by side with an anchored *Phragmites* reedswamp in a fairly sheltered corner of Deep Waters, Wheatfen. Staking showed that the outer edge of the *Glyceria* reedswamp encroached on the open water by an average of 1·4 m. between 17 April 1940 and 6 August 1941; but when the area was revisited in July 1943, it was found that the marginal portion of the *Glyceria* reedswamp had been completely torn away (probably by the exceptional floods of January 1943) to a distance of from 3 to 4 m. behind the stakes, in contrast to the unaffected and still encroaching *Phragmites*. This difference was still more striking in view of the fact that the relative position of the two reedswamps was such that the Phragmitetum was more in direct line with the tidal scour than the Glycerietum and hence subject to greater mechanical force.

In areas where open water is maintained by periodic artificial cutting back of the encroaching reedswamp, drifting masses of hover may be liberated also by this means. Generally, however, the marshmen of the region are especially careful to lift and dry out the reedswamp plants thus cut back, since, owing to the tidal nature of the water, unattached hover masses may return time and time again to the regions from which they were originally cut.

Patches of free-floating hover may become temporarily stationary in several successive places, caught by local shoals or entangled among *Phragmites* reedstools (cf. Pl. 12, phot. 3),

before finally reaching positions where they can obtain firm lateral anchorage. Even while still unattached, they may increase considerably in extent, although their exposure to natural mechanical forces on all sides renders them still more liable to disintegration in this state. A floating *Glyceria* island of this type, originally some 8 m. in diameter, which was noted in October 1939, in a sheltered region of The Bays, Wheatfen, persisted and increased in extent until it was finally removed and disintegrated by the high flooding tides of January 1943 already referred to. A similar, much more extensive island was observed in the summer of 1943 lodged on a shoal towards the northern end of the present Surlingham Broad. This remained in position throughout the winter of 1943–4, but at some time during the following summer became detached from the shoal, and the whole mass

(estimated to be at least 25 m. long by 10 m. wide) drifted about the Broad until, in August 1944, it finally broke up into two separate portions which eventually became lodged in relatively sheltered corners. The ultimate positions of these two portions are shown in Fig. 4 (*A, A'*).

The mechanical disruption of the outer edge of floating *Glyceria* reedswamp is so easily brought about that it can only maintain itself as a primary encroaching agent on open water in those parts where tidal scour is at a minimum. In parts where scour is more intense, it was almost invariably found that the water margin was characterized by an increase in the abundance of anchored *Phragmites* reed-swamp, and it was eventually seen that the relative distribution of *Phragmites* and *Glyceria* reedswamp throughout the area could be largely resolved in terms of tidal scour. This was illustrated very strikingly by the observed distribution of *Phragmites* and *Glyceria* round the margins of the present Surlingham Broad, which
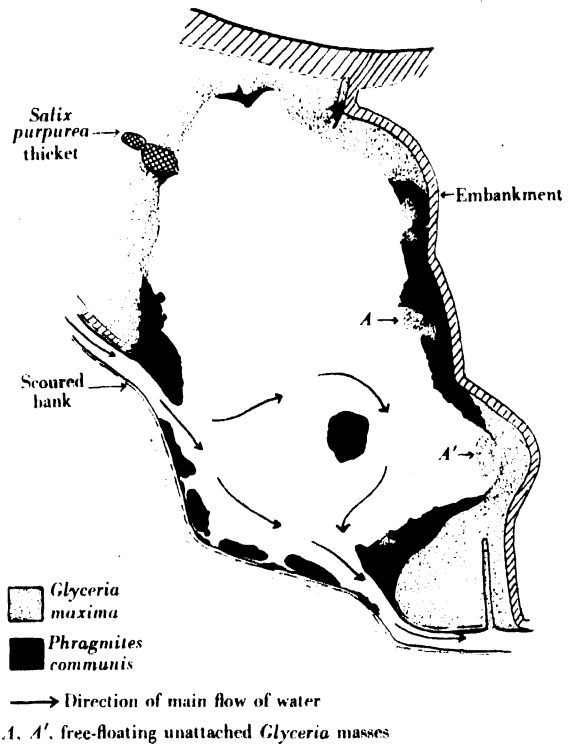

Fig. 4. Sketch map to show the relative positions of *Glyceria* and *Phragmites* reedswamps round Surlingham Broad in relation to tidal scour. Based on a field sketch made from a punt in September 1944.

is illustrated in Fig. 4. (It should be noted that, although in this diagram the scouring action of the current is only indicated as acting in one direction, this is reversed on the turn of the tide; the scour is most intense, however, when the tide is acting in the same direction as the general downflow current of the river, as is indicated by the arrows in the diagram.)

Very good examples of this relationship between *Glyceria* and *Phragmites* reedswamp could also be seen along the central tidal channel of the old Surlingham Broad; here tidal scour is in general acting in a direction at right-angles to the encroachment of the vegetation, and in that part which was surveyed in detail it was seen that there was a narrow and fairly even line of *Phragmites* bordering the channel throughout its length, and sharply delimited from the stretches of almost pure floating *Glyceria* reedswamp

behind it. This line is indicated in the diagrams in Fig. 5. It was found moreover that local changes in the width of this outer band of *Phragmites* could in almost every case be correlated with suspected differences in scouring conditions, as for example a frequent thickening of the *Phragmites* band at the corners of the subsidiary arms leading off from the main channel.

This and other evidence so far accumulated suggests strongly that in the *tidal* system of waterways of the region, the *Phragmites* reedswamp which is present is maintained against the competing *Glyceria* purely by mechanical factors, i.e. *that the sporadic dominance of Phragmites reedswamp has a physical rather than a physiological basis*. The physiological conditions of the habitat appear to be such as to favour the dominance of *Glyceria*, so that when the limiting factor of excessive tidal scour is absent, the anchored *Phragmites* is replaced by the floating *Glyceria* as the primary encroaching agent on the open water. The role played by *Phragmites* therefore appears to be that of a shield protecting the easily disintegrated outer edge of the Glycerietum behind it, which, being thus protected, is able to encroach upon the *Phragmites* fringe from behind as the latter moves forward into open water. This relationship is shown semi-diagrammatically in Fig. 6.

Definite evidence for this encroachment of *Glyceria* on *Phragmites* was given by the two following observations:

(1) A series of borings was made through *Glyceria* hover in area 5 at a distance of about 20 m. behind the *Phragmites* fringe bordering the central channel. Here only an occasional vegetative shoot of *Phragmites* could be seen penetrating the *Glyceria* mat, yet extensive remains of old *Phragmites* rhizomes were found in the underlying ooze (cf. Fig. 6 B).

(2) It was observed that patches of detached *Glyceria* hover frequently become lodged in sheltered bays among *Phragmites* reedswamp; several such patches are shown for Surlingham Broad in Fig. 4. Two which have been under observation since 1943 have shown a definite lateral encroachment upon the surrounding *Phragmites* (although in neither case has the *Glyceria* extended forwards into the open water beyond the 'breakwater' provided by the *Phragmites* on either side).

The actual vegetative mechanism by which *Glyceria* encroaches upon *Phragmites* is of interest. Although the diagrams in Fig. 6 give the impression that *Phragmites* possesses the competitive advantage of greater height over *Glyceria*, this is an apparent rather than an absolute distinction. In actual fact, the vegetative shoots of the latter are almost or equally as long as those of *Phragmites*, but being less rigid and without the support given by deep basal anchorage, they are far more easily prostrated by wind and rain (which are especially effective in these exposed regions). Where these long trailing *Glyceria* shoots abut upon the stiff *Phragmites* fringe, they are supported by the latter in an almost erect position, and the apparent height discrepancy disappears. An additional competitive advantage possessed by *Glyceria* over *Phragmites* is its greater tillering power in the horizontal plane. Moreover it produces new leaf in the spring some three or four weeks earlier than *Phragmites*, a fact which can be correlated with differences in the over-wintering of the two species: whereas, in *Phragmites*, the meristems of the first spring shoots are buried in the substrate throughout the winter, in *Glyceria* the leading shoots of the spring begin their development the previous autumn; these shoots remain small and inconspicuous throughout the winter, but their previous autumnal development results in their meristems being already above the substrate level when favourable growing
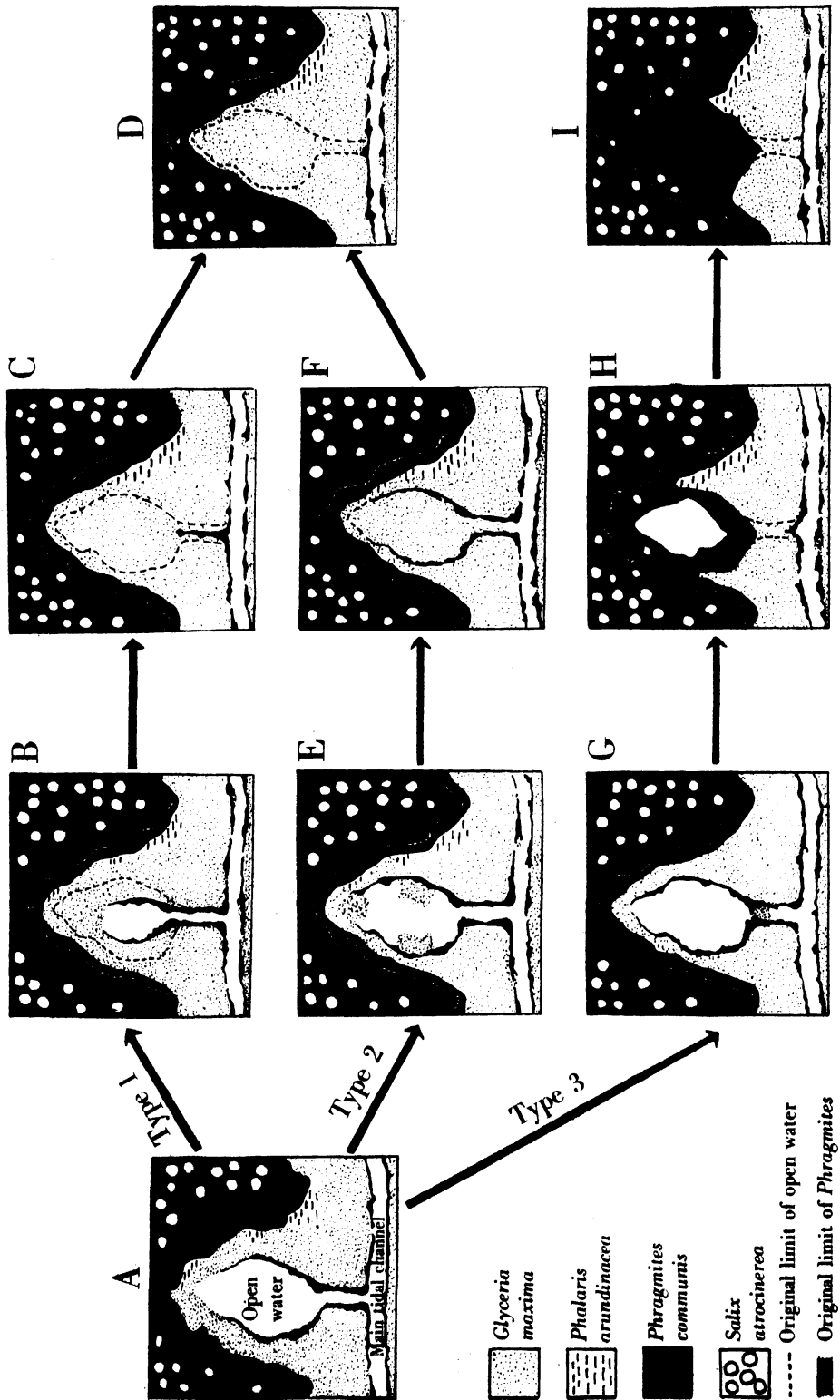
Fig. 5. Diagrammatic representation of successive stages in the filling up of subsidiary arms of Surlingham Broad.

conditions recur in the spring. As a net result of these differences, the general effect seems to be that the tall *Phragmites* fringe is 'smothered out' by the advancing edge of the dense floating *Glyceria* mat in such parts where physiological conditions of the habitat are favourable for the maximum vegetative activity of *Glyceria*.

So far, however, the competitive relationship between *Glyceria* and *Phragmites* has been discussed only for those areas which border open water *under direct tidal influence*. Still further light upon the interrelationships of the two species was given by a more detailed analysis of the various methods by which the subsidiary arms of the Broads are filling up. An interpretation of the various stages encountered both in the Surlingham region and at the lower end of Wheatfen led to the conclusion that open water areas lateral to the main tidal flow could be overgrown by vegetation by three distinct methods. Intermediate and final stages of all these methods could be picked out in both these areas and in similar areas on the other side of the river, and they are reconstructed very diagrammatically in Fig. 5. (It should be noted that though in this figure successive stages are drawn parallel to each other in the three types, no exact correspondence in time interval between them is intended.)

The typical original condition is shown in Fig. 5 A, with the floating marginal mat of *Glyceria* bounded by the protective *Phragmites* fringe (which is frequently absent or interrupted in parts). The later stages in the filling up of such an area may then take place in any of the following ways:

Type 1. The *Phragmites* fringe advances into the open water followed by the floating *Glyceria* mat in the typical manner which has already been described (Fig. 5 B). Eventually, when the whole area has closed up, a thin line of *Phragmites* is left marking the original position of the entrance channel (Fig. 5 C). This line eventually disappears (Fig. 5 D) and the original position of the open water area can only be distinguished from the surrounding fen by the more quaking nature of the *Glyceria* mat in most recently overgrown parts.

Type 2. In this type, floating masses of detached hover, washed into the arm by tidal action, become lodged and increase in extent on the inner side of the fringing *Phragmites* (Fig. 5 E). The latter is left as a gradually disappearing line between the inner and outer *Glyceria* masses (Fig. 5 F), and the ultimate result is as in Type 1. This type of closure is the most common of the three.

Type 3. The open water area becomes sealed off from the main tidal system at some stage before it is completely overgrown; generally this takes place by the extension of anchored *Phragmites* across a progressively narrowing entrance, with the blockage aided by the lodging of detached *Glyceria* hover among the *Phragmites* stools (Fig. 5 G). The entrance of tidal water is cut down and eventually prevented altogether by the rooted reedswamp blocking the mouth of the arm, *and the effect of this is to create physiological habitat conditions which exclude* Glyceria *altogether in favour of* Phragmites. Even though tidal scour is now altogether absent, the latter species now forms the main encroaching agent, *without* a subsequent replacement of the *Glyceria* from behind (Fig. 5 H). The final stage (Fig. 5 I) with originally open water now entirely overgrown with *Phragmites* is typified very well by the large land-locked area (outlined but left white) in area 5 of the folding map. This contrasts very well with the neighbouring *Glyceria*-filled arms where the tidal connexion has persisted. Intermediate stages which aided in the interpretation
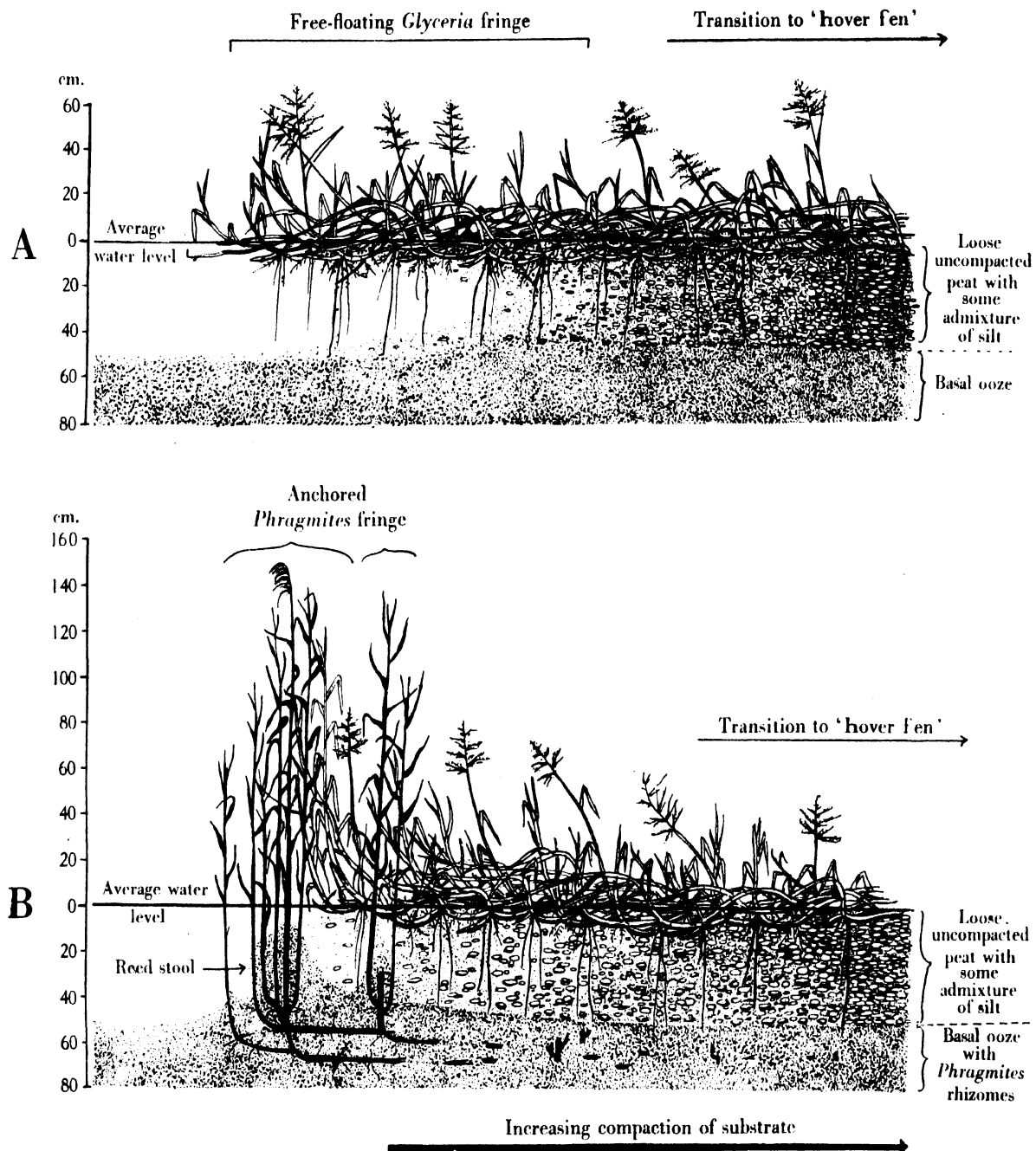
Fig. 6. Semi-diagrammatic bisects of *Glyceria* reedswamps of Surlingham Broad. A, under conditions of minimum scour. B, in regions where scour is appreciable. Based on field sketches made in August 1944.

of this area of *Phragmites* were seen best in certain land-locked pools in that part of the peat basin which lies north of the main river.

To sum up, therefore, it appears that the relative distribution of *Phragmites* and *Glyceria* as reedswamp dominants within the peat basin is primarily determined by the following considerations:

(1) Both species are able to maintain themselves as reedswamp dominants under the peculiar mechanical conditions of the tidal regions (where the lifting effect of the tidal rise is combined with instability of the substrate), but by entirely different growth habits.

(2) In those areas which are under the direct influence of moving tidal water, the physiological habitat conditions are such as to favour the dominance of *Glyceria*, but in parts subject to direct scour, *Phragmites* is maintained as a protective fringe encroached upon later by *Glyceria*.

(3) In land-locked areas within the peat basin, general habitat conditions are less favourable to *Glyceria*, which disappears from the marginal reedswamp region; it is replaced by *Phragmites* which here appears to owe its dominance to physiological factors, the mechanical factor of tidal scour being absent.

(ii) *Other reedswamp species of the primary regions.* The only other reedswamp species found in any abundance in those parts of the Surlingham Broad region where uninterrupted primary colonization was taking place, was *Typha latifolia* L. Though absent in the Phragmitetum, this occurred almost invariably within the Glycerietum. It appeared far more able than *Phragmites* to persist under competition with *Glyceria* in the tidal regions, though it never attained complete dominance in any of the true primary areas apart from a few small local societies within the Glycerietum. It is suggested that this too can partly be explained upon mechanical grounds. Although it has the erect habit of *Phragmites*, its vegetative parts are more buoyant than those of the latter, and it has a less deep-seated rhizome system. Therefore, like *Glyceria*, it is too superficially anchored to resist the twice-daily tidal rise when the substrate is very loose. On the other hand, it cannot adapt itself to these conditions as easily as *Glyceria* by forming a stable floating mat. Its shoots are insufficiently close-set, and its general habit too erect, for it to form a dense encroaching raft comparable to that of *Glyceria* in effectiveness, and although floating *Typha* reedswamps have been recorded elsewhere (Clapham in Tansley, 1939, p. 465), in such cases the disintegrating mechanical factors of tidal rise and fall, and of tidal scour, are presumably absent. Within the Glycerietum it acquires the necessary basal support from the *Glyceria* raft itself; though in those parts of the Glycerietum where *Typha* is at all prominent, the floating raft becomes so treacherous that it is impossible to walk on it with any degree of safety.

In the hinder regions of the Wheatfen area, small anchored reedswamps may be seen completely dominated by *Typha latifolia*, but it is suggested that their presence there may be partly correlated with a more stable substrate in those regions due to secondary opening up and artificial maintenance of the open water in those parts.

The other reedmace, *T. angustifolia* L., is practically absent from the Surlingham area, but is very prominent in certain parts of Rockland Broad, especially towards the southern end. This region has not yet been surveyed in sufficient detail for any suggestion to be advanced in explanation of this.

Scirpus lacustris L., a dominant deep-water reedswamp species of the Broads of the Ant, plays a negligible part in the areas under consideration, one small patch only having

been seen (noted for the first time in August 1943, in the channel between Island Reach and The Bays, Wheatfen). It may be significant that this single patch occurred in an area where the underlying gravel approaches the surface to give a hard bottom to the waterway.

Many of the smaller reedswamp species, more typical of river banks than of the margins of closing Broads (such as *Carex riparia* Curtis and *Acorus calamus* L.) were found bordering those parts of the Wheatfen waterways where a hard bank had been formed at the edge of the water by periodic clearing and deposition of dredgings. These were not thought to form in any sense constituent phases of the primary succession, although it is interesting to note that in several cases *Carex riparia* was found established on the tops of *Phragmites* reedstools in the primary Surlingham areas, and moreover occasionally occurred in the floating Glycerietum, being supported by it in the same way as *Typha latifolia*.

(iii) *Anthropogenic and biotic factors affecting the reedswamps.* Apart from localized clearing of the waterways, the effect of anthropogenic factors on the reedswamp regions appears to be negligible. Reed-cutting was consistently practised in both the Surlingham and Rockland areas until the beginning of the war, but since the reed-haulms are not cut until the winter, when they have dried out, this has no direct effect upon the competitive power of the reedswamp *Phragmites*.

A factor of more recent incidence, at present negligible, but which promises to have a significant effect upon the vegetation unless checked, is the establishment within the last few years of wild populations of coypu (*Myocastor coypus*) within the district. Laurie (1944, unpublished notes) gives the following details: Coypu (or nutria) are large semi-aquatic South American rodents which were first introduced into Britain in 1929–30 and have since been farmed in several parts of the country. From 1933 onwards, various escapes have been reported from such farms, but it is only in Norfolk that they have succeeded in establishing themselves in any number in the wild state. They have now colonized a total of about 40 miles along the Yare and its tributaries, and although they have been practically trapped out in some of the upper reaches above Surlingham since they were first reported from Norfolk in 1943, there is evidence that they are fairly numerous in the fenland round Surlingham, Wheatfen and Rockland Broads. Many of their tracks were seen in the primary areas during the course of the survey. Their feeding habits are such that they cause considerable damage to the reedswamp vegetation, the shoots and rhizomes of *Phragmites*, *Glyceria* and *Typha* all being affected.

(b) The primary fen communities

Where the typical primary succession from open tidal water is uninterrupted, the marginal free-floating *Glyceria* reedswamp behind the *Phragmites* intergrades gradually with a more solid mat of vegetation in which *Glyceria* is still dominant, and which is here designated 'hover fen'. It overlies a loose quaking substrate of peat which has been formed autogenically by the debris of the *Glyceria* raft itself. There is a naturally increasing compaction of the underlying peat at increasing distance from the open water (cf. Fig. 6) so that these hinder fen regions are built upon a more stable basis and there is less freedom of the mat of vegetation to rise and fall with tidal fluctuations. For convenience of expression, the transition from reedswamp to hover fen is arbitrarily fixed as occurring in that region where the substrate has become sufficiently compacted to prevent the

sinking of the mat below the surface of the water when walked upon. The raw peat formed from the plant remains is largely intermixed with silt deposited by tidal water still circulating to some extent below the *Glyceria* mat, so that the percentage loss on ignition for samples of the substrate is lower than might be expected, as is shown by the following values:

Percentage loss on ignition for samples taken below primary hover fen

Depth below surface in cm.	Area 6	Area 7 (western outliers beyond embankment)	Area 41
0–5	84·81	—	—
5–10	85·51	78·98	60·49
10–15	45·45	—	—
15–20	71·35	85·70	45·35
55–75	69·75	—	—

Despite the fact that considerable water movement almost certainly takes place below the fen mat in the proximal regions at least, it is significant that reducing conditions necessary for the formation of peat do exist beneath the Glycerietum. The substrate gives off a strong smell of hydrogen sulphide when disturbed, and immediate diphenylamine tests† made in the field gave uniformly negative results for samples of the substrate taken at various depths, except for an occasional faintly positive reaction in the upper 5 cm. The conclusion can therefore be drawn that Glyceria *acts as a primary peat-forming plant in these tidal areas, and moreover can exist as a dominant under edaphic conditions which are conducive to the formation of peat.* This point will be referred to again later (p. 265).

The Glycerietum is by no means rich in subsidiary species. The dense mat of prostrated living shoots which is typical of *Glyceria* in these exposed parts, even early in summer, forms a very effective barrier against the establishment of seeding species, and even those which do occur are of limited distribution and abundance. The following list is compiled from five different areas, each being between 2000 and 5000 sq. m. in extent, of typical primary Glycerietum from both the Surlingham and Wheatfen-Rockland regions. The numbers 2–5 following the species represent the constancy of the individual species within the five areas examined; those recorded only from a single area are omitted. The species are arranged in approximate order of abundance within each constancy group, and those marked with an asterisk are types which are in general only characteristic of the hinder, more stable regions of the Glycerieta.

Glyceria maxima (Hartm.) Holmb.	5	Peucedanum palustre Moench	2
Typha latifolia L.	5	*Galium palustre L.	2
Solanum dulcamara L.	5	Polygonum amphibium f. terrestre Leers	2
Phragmites communis Trin.	5	*Sium erectum Huds.	2
*Epilobium hirsutum L.	5	*Eupatorium cannabinum L.	2
*Urtica dioica L.	5	*Calystegia sepium Br.	2
Caltha palustris L.	5	Typha angustifolia L.	2
Rumex hydrolapathum Huds.	4	Humulus lupulus L.	2
		*Galium aparine L.	2
*Phalaris arundinacea L.	3		
Carex riparia Curtis	3		
Cicuta virosa L.	3		

† The diphenylamine test was that employed by Pearsall & Mortimer (1939, pp. 484–5) to give some indication of the presence or absence of oxidizing substances in the soil. Diphenylamine sulphate in concentrated sulphuric acid is added to a small sample of the soil on a white spot plate, and the development of a blue colour indicates that oxidizing substances are present.

The primary fen Glycerietum forms a fairly broad band, but in its hinder regions it is encroached upon by *Phragmites*, which in addition to its presence in the reedswamp regions also forms a definite constituent phase in the fen succession; it here has a much more stunted appearance than in the reedswamp. The fen Phragmitetum appears to advance upon the Glycerietum entirely by vegetative means, so that there is a fairly distinct and continuous line between the two, the transition zone being relatively narrow. This rather significant replacement of *Glyceria* by *Phragmites* in the later stages of the prisere may be explained on the evidence that has already been discussed as to the relationships between the two species. It has already been shown that *Glyceria* can only become dominant to *Phragmites* in those regions of the peat basin which are served by moving tidal water, and that in land-locked areas their mutual relations are the reverse. In the hinder regions of the primary fen, where the substrate is more compacted, the circulation of tidal water below the fen mat is greatly restricted and physiological conditions therefore gradually change with increasing distance from the open water to favour the dominance of *Phragmites*, which is therefore able to encroach upon the Glycerietum from the rear. It is not thought that the relationship between these two species is in any way controlled by the actual building up of the substrate and concomitant changes in vertical relationship to the general water table. The tidal rise and fall ensures that even at this stage the substrate is waterlogged throughout the summer, and moreover observations from other areas show that *Phragmites* and *Glyceria* have approximately the same upper limit in relation to the water table.

A direct comparison might here well be made with corresponding priseres in other east Norfolk Broads. The evidence from the area under consideration suggests very strongly that *the Glycerietum of the tidal Yare valley Broads does not appear to correspond with the Cladietum of those of the Bure valley, by implication following the Phragmitetum, as has previously been suggested (Tansley, 1939, p. 654), but rather to be an interpolated successional phase within the limits of the zone which, in areas with less water movement, would be occupied throughout by* Phragmites.

Some note should perhaps here be made of the position occupied by *Phalaris arundinacea* L. in relation to the general scheme within these tidal areas. Pallis (1911) describes *Phalaris* as co-dominant with *Glyceria* in these regions, but it was found during the course of the present survey that the former was by no means as widespread as the latter, and moreover that when it did attain any degree of dominance, it tended to occupy its own characteristic zone within the prisere, intermediate in position between the fen Glycerietum and the advancing fen Phragmitetum.

The Phragmitetum carries a much more prominent subsidiary flora than the Glycerietum, both in abundance and in number of species. The following list, compiled on the same lines as the previous one, shows this difference:

Phragmites communis Trin.	5	Galium palustre L.	4
Filipendula ulmaria Maxim.	5	Lathyrus palustris L.	4
Calystegia sepium Br.	5	Carex riparia Curtis	4
Lysimachia vulgaris L.	5		
Angelica sylvestris L.	5	Calamagrostis canescens (Wigg.) Dr.	3
Iris pseudacorus L.	5	Thalictrum flavum L.	3
Carex paniculata L.	5	Rumex hydrolapathum Huds.	3
Caltha palustris L.	5	Stachys palustris L.	3
Epilobium hirsutum L.	4	Sium erectum Huds.	3
Phalaris arundinacea L.	4	Urtica dioica L.	3
Mentha aquatica L.	4	Typha latifolia L.	3
Lythrum salicaria L.	4	Carex acutiformis Erhr.	3

Eupatorium cannabinum L.	2	Humulus lupulus L.	2
Vicia cracca L.	2	Scutellaria galericulata L.	2
Solanum dulcamara L.	2	Polygonum amphibium f. terrestre Leers	2
Peucedanum palustre Moench	2	Valeriana officinalis L.	2
Lathyrus pratensis L.	2	Rumex conglomeratus Murr.	2

This increase in the subsidiary flora is probably not only related to increasing compaction and dryness of the substrate, but also to the difference in the vegetative habit of the dominant. In contrast to the dense mat of prostrate *Glyceria* shoots, *Phragmites* has a much more erect habit and bare peat can frequently be seen between the vegetative shoots. The stunted habit of *Phragmites* in this region, and the relatively small leaf expanse, allow a considerable penetration of light to this peat surface, and the establishment of subsidiary species with the Phragmitetum is also probably aided by the late production of new leaf by the latter in the spring (cf. p. 239).

(c) *The establishment of carr*

Since this survey was primarily carried out with a view to determining the relationship of *Glyceria* within the area, the later stages of the succession have not yet been followed out in very much detail. Moreover, whereas the primary Glycerieta and parts of the Phragmiteta of the Surlingham region have generally been regarded as too unstable and inaccessible to be mown, certain of the regions farthest from the open water, where the substrate is relatively firm, have been subjected in the past to some annual cutting, and the encroaching carr has to some extent been cleared. In one or two areas, however, where such records as were available showed that past clearing and cutting had been absent or negligible, stages which were thought to represent the later phases of the direct primary succession were encountered.

As a general rule carr establishment only begins within the fen Phragmitetum, with colonization by isolated bushes of *Salix atrocinerea* Brot. The Glycerietum is occasionally invaded by this species, but the general absence of carr outliers here may possibly be as much due to the greater resistance offered by *Glyceria* to the establishment of seeding species as to the substrate conditions within this region. The latter is sometimes characterized by the presence of bushes of *Salix purpurea* L., which frequently occur near the outer edge of the Glycerietum; it is suggested that these bushes may possibly owe their initial establishment to the tops of the *Phragmites* reedstools, which are uncovered by the tide for the major part of the day, but direct evidence on this point is not yet available.

Salix atrocinerea is however very obviously the chief pioneer species of carr establishment, and is moreover easily the most prominent woody species over the whole area. Within the open sallow carr, *Phragmites* remains the dominant constituent of the ground flora, but subsequent closing of the carr is marked by a considerable increase there of *Carex paniculata* L. and an intrusion of *Alnus glutinosa* Gaertn. into the woody layer. This leads in some parts at least to a Saliceto-Alnetum with *Carex paniculata* very abundant in the field layer.

Later stages in the succession have largely been lost by human interference, but in one or two areas at least a further progression could be traced to pure alder carr. The most convincing evidence for a direct succession of this type was afforded by area 8, where zoned stages corresponding to those already described could be seen. The southern

corner of this area is occupied by a closed alder carr with dying *C. paniculata* tussocks and bare areas of peat between the alder bases; frequent pools of water could be seen between the remains of the tussocks. This type of carr corresponds with that which Pallis (1911) has previously distinguished as 'swamp-carr' and which she has regarded as genetically distinct from 'fen-carr', Godwin & Turner (1933, footnote, p. 243) have however suggested that field evidence from the Calthorpe Broad region indicates that alder carr of this nature may form a normal phase, following pioneer sallow, of the direct succession from fen, the exposure of a free water surface among the alder bases being concomitant with a sinking of the peat surface itself beneath the weight of the invading carr. This explanation would be especially feasible in the case of the Surlingham area, where the fen mat is developed from an originally floating reedswamp with only slow consolidation of the peat below it.

The evidence for regarding the alder carr of this area as part of a true primary succession within the Surlingham basin is mainly as follows:

(1) The position of the area in relation to the general direction of the closure of the Broad is such that it appears to have been formed by a comparatively recent encroachment on the open water.

(2) A progressive consolidation of the peat beneath the surface mat can be traced from the Glycerietum at the edge of the open water to the carr itself. The dense vegetation mat in the fen regions gives a somewhat false stability in these parts, but it is underlain by a very soft peat, which is revealed by the breakdown of the surface mat under the closed canopy of the Alnetum.

(3) The establishment of *Carex paniculata* in the Phragmitetum, the presence of much larger and more abundant tussocks throughout the Salicetum and the Saliceto-Alnetum, and the remains of dying tussocks in the Alnetum, provide circumstantial evidence that the latter is developed as a successive phase to the preceding stages.

(4) Records so far available indicate that towards the eastern half at least human interference within this particular area has been at a minimum.

Young alder carr of a different type was found at the south-west corner of the old Broad (area 1). Here, a fairly extensive area of fenland was dominated by *Juncus subnodulosus* Schrank with open alder carr developing within it. The vegetation of this area was not thought to correspond with any stage of the direct primary succession already outlined, but to be secondary in origin; its more detailed consideration will therefore be left to a later section.

(3) *Modifications of the general scheme within the Wheatfen area*

A general successional scheme from reedswamp to carr having been elaborated for the primary regions of Surlingham Broad, it was found possible to apply the same principles to an interpretation of the more difficult relationships of the main communities at Wheatfen. Here, as already indicated, much of the open water has been maintained artificially far beyond its natural existence. Towards the south end of the chain of waterways many of the marginal reedswamp and fen communities are obviously primary in origin, with the underlying peat soft and unconsolidated; but, farther back, the northern pools have been maintained as hollows inset in much older peat which under natural circumstances bears carr. As may be seen from the folding map, uncleared carr abuts

immediately upon open water round most of these pools; such fen communities as are present are anthropogenic in origin and belong more properly to the next section.

The majority of the Wheatfen waterways, though superficially similar to those of the old Surlingham Broad in the distribution and extent of residual open water, cannot therefore be directly compared with them as regards either the age or status of the surrounding vegetation. In contrast to the wide marginal semi-floating Glycerietum of the Surlingham area, at Wheatfen many of the residual pools are bounded by a hard 'rond' of consolidated peat, which may in parts be raised by deposited dredgings. Anchored *Phragmites* reedswamps or floating *Glyceria* hover frequently become established along the margins of these pools, especially in the parts nearest Rockland Broad. Owing to frequent clearing, however, they have a very sporadic distribution, and no direct connexion with the vegetation of the rond behind them. In many cases this results in the apparently anomalous situation of a floating *Glyceria* reedswamp abutting directly upon mature carr developed on deep compacted peat.

Much of the carr at the extreme distal end of the chain, in the region of Avenue Pool, is of the 'swamp' type, with *Salix atrocinerea* and *Alnus glutinosa* both abundant. It is suggested that this carr represents the Saliceto-Alnetum stage of a primary succession which was initiated by the original retreat of the open water in the direction of Rockland Broad, but whose later stages have been brought into juxtaposition with tidal water by the artificial backward extension of the waterways already noted.

The opening up of these hinder regions has incorporated into the tidal system again certain small overgrown land-locked pools which were apparently left behind by the original retreat of the open water. These pools are not marked on the old Tithe maps of 1840 (Fig. 3); they probably existed but were overlooked in the dense tangle of vegetation. According to Mr Cockle the presence of Mystery Pool was only discovered as a result of marsh-burning in 1920, and it was not opened up until some years later. The marginal vegetation of these pools now consists largely of *Phragmites* with a considerable amount of 'tussock-swamp' of species such as *Carex paniculata, C. riparia, C. acutiformis* and to a lesser extent *Cladium mariscus* R.Br. Although they are now under tidal influence, *Glyceria* is noticeably absent as a constituent of the reedswamp, but the time interval from the opening up of these pools with the main waterways has not yet been sufficiently long for the vegetation to have become stabilized. The absence of *Glyceria* is probably partly due to the resistance offered by the twisting waterways to the passage of floating hover, and partly to the considerable shading effect of the marginal carr. *Glyceria* does not propagate itself at all readily by seed, and the extent to which floating hover *may* have been removed artificially from these areas is not known.

Taking the past history of the areas into consideration, the evidence from both Wheatfen and Surlingham does not conflict with the suggestion that 'swamp-carr' may be genetically derived from 'fen-carr' as at least one expression of the later stages of the direct primary succession within the area. Whether closed-canopy alder carr represents the ultimate or penultimate stage of the hydrarch succession within the region cannot yet be estimated; moreover, it is very probable that these later stages which have been tentatively outlined operate in parts of the peat basin only. Ash is very prominent among the sallow in many parts of the Wheatfen area, and Ellis (1934) has suggested that the general succession leads from fen through sallow-ash carr to ultimate oak-ash woodland. The carr areas must be surveyed in far greater detail, and the structure and composition

of their underlying peat carefully examined, before any general conclusion can be drawn: but the foregoing observations, though somewhat incidental to the main purpose of the original investigation, have been included as providing an interesting correlation with the methods of carr re-establishment in the secondary fen areas, which will be dealt with in the next section.

D. The secondary anthropogenic fen communities

(1) *The general characteristics of the chief areas involved*

During the course of the survey it became increasingly obvious that anthropogenic factors of the habitat were of paramount importance, not only in determining the maintenance of fen in areas which would otherwise be occupied by carr, but also in the minor detail of the actual distribution of the main fen dominants themselves within the general pattern of these secondary areas. The necessity for a detailed consideration of the part played by the past history of the economic utilization of fen areas in any interpretation of the present distribution of their vegetation has already been admirably illustrated for Wicken Fen (Godwin *et al.* 1929*a*, 1929*c*, 1932, 1941). Here it was shown that the distribution of *Cladium mariscus* and *Molinia caerulea* as dominants could in many cases be directly correlated with relative intensity of past cutting of different strips of the fen. The principle of deflected succession, elaborated by Godwin (1929*b*) and worked out within the Wicken area, was found to have equal application in the Yare valley fenland, though different species are involved.

The major part of the secondary fen areas in the region of Rockland and Surlingham Broads consists of 'mowing marsh', i.e. areas which have been cleared of carr and which have been maintained as fen by annual mowing by hand. In addition, a few areas of the older peat have in the past been better drained than others and maintained as rough grazing land.

The general drainage conditions operating within the area may be classified as follows:

(1) The dykes intersecting the peat are entirely open to the river, allowing free ebb and flow of tidal water within them. This system is in future referred to for convenience as the 'open-dyke' system. It has the advantage of ensuring a general circulation of water throughout the areas in which this system operates, thus preventing the stagnation of water in hollows, but it has no permanent effect upon the lowering of the water table. Although the surface of the peat is slightly above the average summer high tide level, these areas are frequently flooded in winter. They are too wet for grazing purposes and consist entirely of mowing marsh, except in certain small regions towards the westward edge of the peat basin on which stock have occasionally been allowed.

(2) The dykes forming a closed system within any one area, with no open connexion with the tidal river. These areas are embanked to prevent lateral flooding by master tides, and the level of the water in the dykes is, or has been, subject to some measure of control by sluices or pumps. Areas served by this 'closed-dyke' system have been used for summer grazing, varying in intensity in different parts of the region. Areas 53 and 54, south of Rockland Broad, which are drained by a turbine pump, are still regularly grazed; areas 10–13, in the neighbourhood of Coldham Hall, were previously served by a pump, but this was removed in 1914 and replaced by sluices which are now in varying stages of disrepair; area 14 was in the past also sluiced, but the outlet from this has been completely

blocked for many years, so that the dykes now act purely as sumps; area 7, within the main bend of the river, was also pumped in the past, but the pumping system has been removed and not replaced by sluices, and the whole area is derelict.

The interrelationships of the plant communities of the 'closed-dyke' areas naturally offer a far more complex picture than those of the mowing marsh. Not only has the factor of grazing a far more modifying influence on the relative dominance of individual species than that of annual mowing, but in addition it can be seen that there is far less uniformity in general drainage conditions here than within the mowing marshes. It is shown in subsequent pages that areas served by the 'open-dyke' system could be related to a general plan with only minor modifications due to degree of overgrowth, number and relative positions of the dykes themselves: in contrast, the drainage systems of the previously grazed areas are in such varying stages of disrepair and dereliction that no common basis now exists between them. The present drainage conditions in these latter areas range from those in which there is still effective lowering of the water table by pumping (as in areas 53–54), through types in which occasional or persistent wedging open of the sluice gates through disrepair gives rise to conditions approximating to those of the 'open-dyke' system (as in areas 10–13), to a final stage in which there is now no outlet at all for the water accumulated in the dykes (as in area 14). It was felt therefore that a further consideration of the plant communities of such areas could not profitably be incorporated into the general scheme until more evidence is at hand; the further discussion of the secondary fen communities will therefore be limited at present to those of the mowing marshes, which occupy by far the greater part of the area surveyed.

(2) *The communities of the mowing marsh*

(a) *Detailed consideration of the drainage system of the mowing marsh*

The strip of secondary fenland between Rockland Broad and the Coldham Hall Ferry consists almost exclusively of mowing marsh and is served throughout by the 'open-dyke' system. There was however found to be considerable variation between the individual areas of this section as regards their relation to the influence of tidal water. This depended upon both the distribution and abundance of the branches of the 'open-dyke' system and upon their present state as regards blockage by overgrowth; the dykes require frequent clearing to keep them open, and relaxation of this in many parts (especially since the beginning of the war) has resulted in considerable restriction, and sometimes complete inhibition, of water circulation within them.

The strip of peat at present under consideration is intercepted by a number of parallel dykes running back at right angles to the river and joined by cross-branches. Three distinct types of arrangement are prevalent, which are represented in Fig. 7. Either the main dykes running back from the river are close together (Fig. 7 A), with only a narrow strip of fen peat between them, as in areas 15, 25 and 40, or else they are more widely spaced (Fig. 7 B, C) but with the intervening peat intercepted by additional branches running at right angles to the dykes of the first order. When these secondary dykes are numerous and close together (Fig. 7 C, areas 17 and 35) the resultant effect is very much as in the case with the long narrow strip; in many areas, however, the dykes are farther apart (Fig. 7 B, areas 18–19, 21, 27–29 and 43), so that relatively large blocks of peat are cut off.

A further modification, which may apply to any of the above types, is the presence of an embankment of dredgings along the river itself. In a few strips only was such an embankment absent, with the lower end directly open to winter flooding (as in areas 35 and 39); in the other riverward areas (areas 15, 17, 19, 21, 24, 25, 29, 34, 40 and 43) an embankment was constantly present, so that in these areas the flooding of the peat strips in the winter takes place laterally from the dykes only. The two arrangements, therefore, produce certain minor differences as to the regions of most extensive silt deposition by the flooding water.

A similar modification on a much smaller scale is produced by the deposition of the originally excavated peat, and of subsequent dredgings, on the banks of the dykes themselves. In most cases winter flooding has largely dissipated such material over the intervening fen, but in one or two areas where it was found that one side of a dyke was slightly higher than the other, such inequalities were thought to be due to original positional differences of such excavated peat and dredgings; these differences naturally
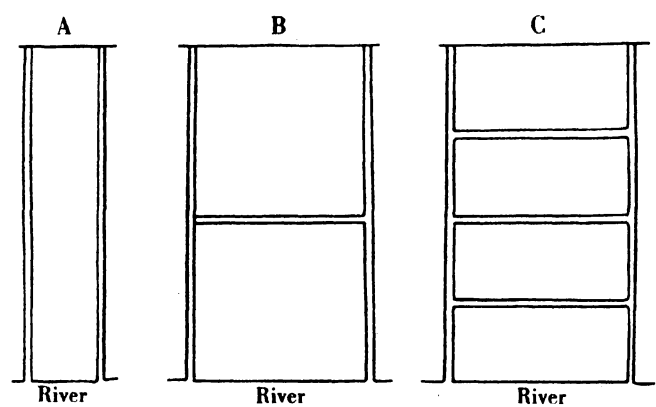

Fig. 7. Diagram to indicate different dyke arrangements within the mowing marsh areas.

affect the extent of tidal flooding and silt deposition on the two sides of the dyke, and had to be taken into consideration in any analysis of the community relationships.

Silt deposition is naturally most extensive at the dyke edges, so that the peat there is intermixed with a considerable amount of inorganic material which decreases with increasing distance from the dykes. This is well shown by the following percentage loss on ignition values for areas 19 and 34. The approximate positions of the samples from these two areas are shown in Fig. 8.

Percentage loss on ignition for soil samples from secondary fen areas

Depth in cm.	Samples taken from near dykes			Samples taken from intervening fen		
	1	3	4	2	5	6
10	67·06	59·75	52·33	83·75	85·81	87·38
25	66·01	57·70	86·37	80·40	84·80	82·19

The high inorganic content of the substrate near the dykes is naturally only found in the upper layers. The deeper layers of peat, formed long before the dyke was cut, are intermixed with a far smaller proportion of silt, and the percentage loss on ignition naturally increases at the greater depths. This is well illustrated by the following table

of two series of samples from another area, taken near each other at approximately 10 m. from the edge of the main dyke:

Percentage loss on ignition at different depths near dyke in secondary fen area

Depth in cm.	Series 1	Series 2
0–5	63·0	56·3
5–10	56·3	47·2
10–15	74·7	45·5
15–20	75·3	53·3
20–25	78·2	81·4
25–30	84·7	84·1

The high value for the 25 cm. sample in set 4 of the previous table can probably be accounted for on these lines.
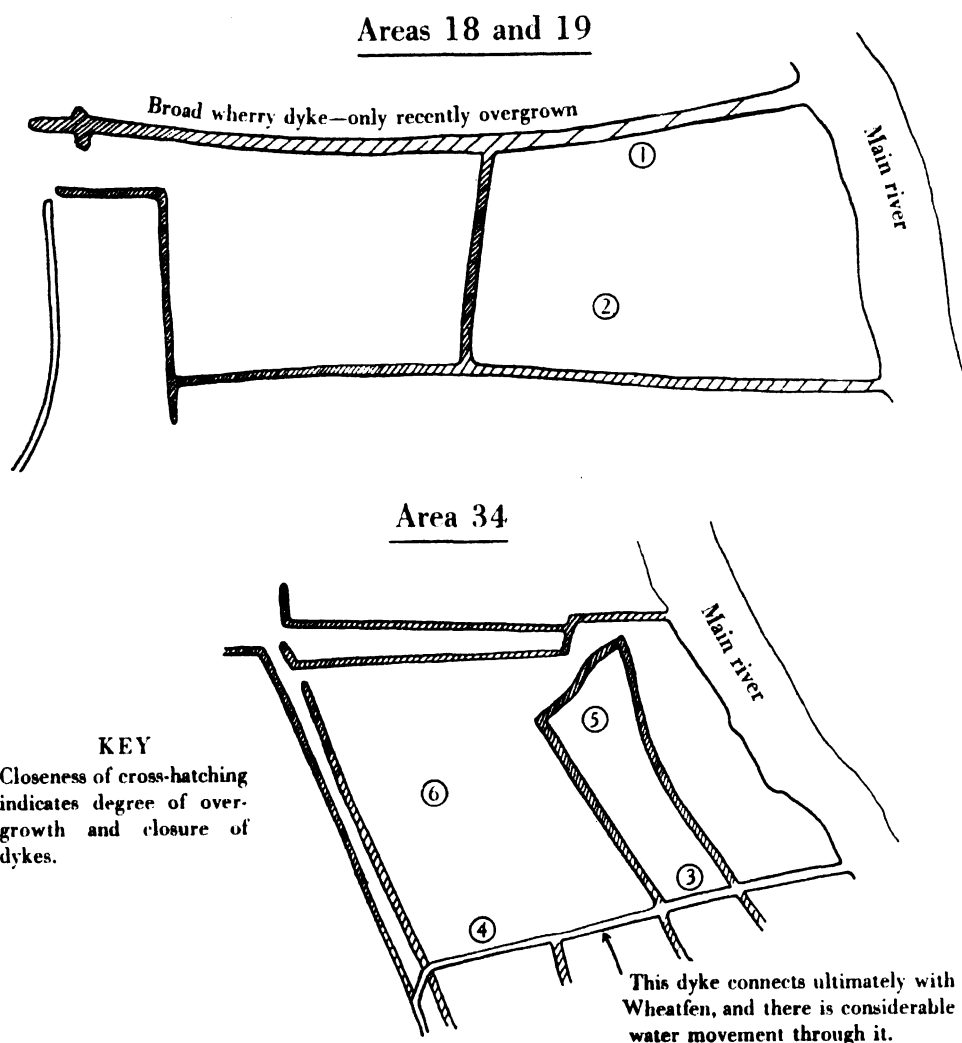
Fig. 8. Sketch maps to show positions of soil samples in relation to the dykes.

The greater deposition of silt near the dykes would suggest a definite increase in the height of the substrate in these regions, resulting in a slight concavity of the fen surface between the dykes. Direct measurements of this were not made, but it was observed

that water tended to collect towards the middle of the peat strips and to be drained more readily from the marginal regions abutting on the dykes.

Diphenylamine tests (see footnote, p. 245) made in August and early September 1944 in general gave a strongly positive reaction for samples from the upper 10 cm. near the dykes, but only a faintly positive one for similar samples taken from the centre portions of the strips. At 25 cm. faint or negative reactions were generally recorded from both regions.

No detailed observations have yet been made upon the extent of seasonal and diurnal fluctuations of the water table within the strips of secondary fen. It is obvious that the proximity of the water table to the fen surface is not only dependent upon variations in the absolute height of the latter in different parts of the fen, but also upon the relative distance of these parts from the tidal dykes, the size and condition of such dykes, the ease of lateral water movement through the substrate in various regions, and actual variations in the range of the tidal fluctuation itself on different days. General observations however indicate that although the upper layers of fen peat are wet to the touch throughout the whole summer, the water table is itself in general nearer the surface and less liable to diurnal fluctuation in the centre of the peat strips than towards their edges. This contrast between the maintained water table of the central portions, and its more variable relationship to the peat surface towards the dykes, is reflected in the results of the diphenylamine tests already mentioned.

In the absence of direct detailed evidence, it is tentatively suggested from general observations that the same relationship of the water table to the fen surface may be applicable in considering the whole of the peat strip in relation to the river itself: the proximal riverward portions of this strip give the general appearance of being slightly higher and better drained than the landward distal portions, in several parts of which there is a standing water table above the surface of the substrate throughout the entire summer. A gradual slope of this nature in the actual fen surface would be expected from a consideration of the regions of most intensive silt deposition from the river water, but it has yet to be confirmed by direct measurement.

Dykes at all stages of neglect and overgrowth were found within the area, and a very complete series could be traced from those which were still open throughout their length to those in which the filling up process was so far advanced that their original position was only indicated by a slight depression in the fen surface. The series is diagrammatically represented in Fig. 9, and it is described in some detail as giving additional support to suggestions already put forward as to the interrelationships of *Glyceria* and *Phragmites* within the peat basin.

Those dykes which remained sufficiently open to permit of tidal circulation within them were found to be invariably bordered throughout their length by *Glyceria*: this plant is the main agent in their initial overgrowth, its trailing shoots forming a floating hover mat over the surface of the dyke, cf. Pl. 12, phot. 4. Such a mat is essentially similar in structure to the floating *Glyceria* reedswamp already described, and rises and falls with the tide in the same way. Since scour is more intense at the proximal end of the dyke, the formation of the mat and subsequent silting and peat deposition beneath it take place from the distal end downwards, so that this end may be completely closed while the riverward end is still open (Fig. 9 B).

As water circulation in the hinder regions of the dyke is cut down, there is a gradual encroachment of *Phragmites* from this end; this advances along the original channel of

the dyke (Fig. 9 C–E) until it eventually occupies the whole of it with the exception of a small residual patch of *Glyceria* at the extreme riverward end, which appears to persist indefinitely (Fig. 9 F). The role of *Glyceria* as the main coloniser of the tidal open water, and its succession by *Phragmites*, is therefore reproduced in miniature.

A further correlation with the interrelationships of the two species already outlined is that, in addition to the encroachment of *Phragmites* with the cutting down of tidal circulation, another small band of *Phragmites* was invariably found fringing the lower riverward end of the dyke in the region of the most intense scour (Fig. ⁰ B–D). This band persists until the dyke becomes sufficiently overgrown for the scour to become negligible (Fig. 9 E, F) and it is thought that its original maintenance against the *Glyceria* mat developed farther up the dyke is due to purely mechanical factors of the habitat in exactly the same way as already indicated for the advance fringe of *Phragmites* in the more extensive primary regions.
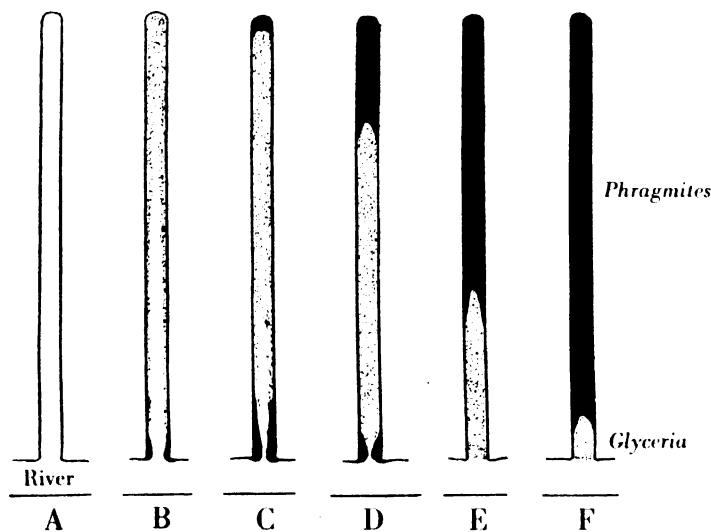

Fig. 9. Stages in the filling up of the tidal dykes.

(*b*) *The extent of past and present cutting of the mowing marsh areas and its effect on the dominants*

In the past, the majority of the fenland was very extensively cut to provide both winter fodder and litter, not only for local use, but in many cases for transport to other towns; according to local report, much of the better quality 'marsh-hay' was in the last century sent to London for cab-horses. Increasing labour costs have however seriously restricted the harvesting of the 'marsh-hay' crop and, although a few areas were still cut regularly up to 1939, such cutting has been intermittent and irregular within the region as a whole for many years, and in several parts carr is already re-establishing itself to a greater or lesser extent.

The two main species of the unexploited primary fen regions—*Glyceria* and *Phragmites* — form extensive communities over the mowing marsh regions, but in addition *Juncus subnodulosus*, which is practically absent from the prisere, replaces the other two in many

parts of the fen. Of these three chief dominants of the secondary fen, *Glyceria* itself is generally reckoned to provide the most valuable hay crop. It has long been recognized both in this country and abroad as a nutritious fodder grass, much relished by stock (Curtis, 1777, etc.). As green fodder or winter hay, it is generally cut young, before the emergence of the panicle, while later growth can be cut again for litter. Records for both Britain (Curtis, 1777; Deakin, 1871) and for the Continent (Lecoq, 1844) show that it can be cut as much as thrice in one season. This resistance to intensive cutting shown by *Glyceria* may be correlated with its considerable tillering power, and is an important factor in determining the extent of its distribution within the mowing marsh.

Richards & Clapham (1941) indicate that *Juncus subnodulosus* also is very tolerant of frequent cutting and that this fact gives it a definite advantage within mown areas over taller but less tolerant species such as *Phragmites*. The susceptibility to summer cutting shown by *Phragmites* may be correlated with the fact that it appears to have less tillering power than *Juncus* and *Glyceria*, and that it attains its maximum vegetative development considerably later in the year than either of the other two species.

(c) Estimate of the relative effect of drainage conditions and of cutting on the distribution of the dominants

The distribution and present condition of the dykes themselves, as noted by direct observation during the course of the survey, was thought to afford a reasonably good basis for any analysis of the distribution of the dominants in relation to the influence of tidal water and its concomitant effect on regions of silt deposition and water movement. The extent of past and present cutting and its effect on the distribution of the species was far more difficult to assess, and although the many land-owners who were consulted were very ready and willing to give such details as they were able, the information gained was in most cases far too incomplete to be used as critical evidence. The main difficulties attending the compilation and use of such evidence may briefly be summarized as follows:

(1) In very few cases only was it possible to trace the past economic history of any one area back for a sufficient length of time, the usual limit being some 10–20 years.

(2) The treatment in each area varied greatly in most cases from year to year, according to different requirements of the owner; in many cases the treatment changed with change of ownership.

(3) Treatment varied not only from area to area, but also within different parts of a single plot according to requirements and available labour.

(4) The actual season of cutting of individual areas varied from plot to plot, and from year to year within the same plot, depending upon the purpose for which the crop was required. Hay needed for fodder would be cut relatively early in the year, while litter was cut at any time from July to October, according to the weather and convenience of the owner. In one or two areas, the reed was cut for thatching, and such cutting would not be carried out until the winter, when the overground parts of the plants were already dead and dry. Since, as has already been pointed out, there is considerable variation in the time of maturation of the individual species, late and early cutting would have different proportional effects on the species; early cutting would be expected to favour *Glyceria* and *Juncus* against *Phragmites* to a much greater degree than late cutting.

(5) Relaxation of cutting was in many cases concomitant with neglect and overgrowth of the dykes, and it was difficult to assess the relative effect of the two factors in such cases.

Nevertheless, despite the unsatisfactory and highly circumstantial nature of such evidence as was available, it was found possible to formulate certain suggestions as to the effect of summer cutting on the vegetation, and to some extent to correlate the present distribution of the vegetation with this as well as with the drainage conditions. The resulting suggestions are summarized below, with some indication as to the main areas from which the evidence was taken.

(1) Summer cutting tends to maintain *Glyceria* and *Juncus* against the taller *Phragmites*, the proportion of *Phragmites* to the sum total of the other two being generally greater in those areas in which it is known that cutting has been relaxed for many years. The best evidence for this comes from certain similar areas lying on either side of a common dyke, where differences in drainage conditions are to some extent eliminated, e.g.

Area no.	Previous history	Vegetation
40	Regular summer cutting until 1942	Dominated by *Glyceria*
39	Subjected to winter cutting at lower end for thatch only	*Phragmites* dominant over major part, with only a little *Juncus* at western end and thin band of *Glyceria* filling up southern dyke
23	Cut annually for fodder and litter until about 10 years ago. Still cut along dyke sides	*Glyceria* dominant to *Phragmites* over the greater part
21	Let for shooting and not cut for at least 20 years (probably longer)	*Phragmites* dominant over greater part. *Glyceria* confined to narrow band along dykes

Moreover, it has been noticed that even within the last six years there has been a tendency for *Phragmites* to increase at the expense of *Juncus* in area 28, in which cutting has now been completely relaxed. According to local marshmen, relaxation of summer cutting for several years is invariably accompanied by increase of reed, and it is reported from several separate sources that there is now much more reed over the area as a whole than was present two or three decades ago, when the fens were far more extensively cut. There is moreover some evidence, too detailed and scattered to be recorded here, that with regular cutting *Phragmites* may be eliminated altogether as a dominant from the secondary fen.

(2) The dominant species of the secondary fen show a very definite zonation in every area in relation to the influence of tidal water. *Glyceria* invariably occupies those stretches of the peat immediately abutting upon the tidal dykes, and the zone of *Glyceria* tends to increase in width towards the riverward end of the peat strips. *Juncus*, on the other hand, is confined to the centre of the peat strips where the fen surface is thought to be slightly lower and less well-drained and where silting and water movement are at a minimum; it becomes most abundant at the landward side of the peat basin where there is considerable standing water and where tidal influence is least effective. When present, *Phragmites* occupies an intermediate position between the other two, the width of the *Phragmites* zone in relation to the others being determined by the intensity of cutting as already indicated. This zonal distribution of the three species in relation to tidal

influence is so uniform and consistent over the whole region that it is unnecessary to quote definite areas; it may be summarized in the following diagram:

Increasing intensity of summer cutting
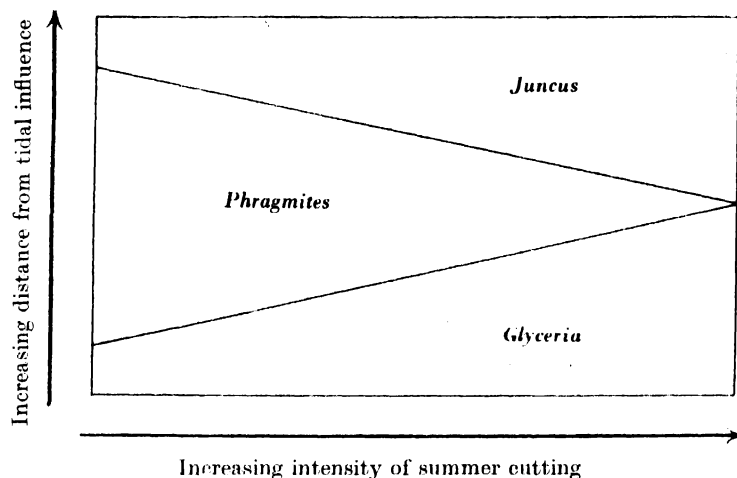
Though the balance existing between the three species is thought to be to some extent determined by cutting intensity, nevertheless the ultimate extent of the encroachment of *Phragmites* into the Glycerietum and Juncetum appears to be limited by edaphic conditions. Even in areas which ha♥e not been cut for some 20-30 years the open dykes still retain a narrow band of *Glyceria* along their margins, and it is probable that *Juncus* may maintain itself to some extent against *Phragmites* in the same absence of cutting. The evidence so far available tends to show that although certain of the more riverward Junceta may be eliminated directly by *Phragmites*, such encroachment is so slow in the hinder regions of the fen strips that the Junceta of these parts may revert directly to carr without an intermediate re-establishment of *Phragmites*.

Bush colonization appears to take place more easily within the Juncetum than within the Phragmitetum, but to be inhibited within the Glycerietum (this point will be referred to later on p. 262). The main woody colonizer is again *Salix atrocinerea* over the major part of the fen, but in the hinder Junceta the *Salix* bushes may be accompanied or replaced by *Alnus glutinosa*.

The general course of events which is thought to take place in a typical fen strip on relaxation of cutting or overgrowth of dykes is shown in Fig. 10. This figure is based on the sum total of the evidence so far available from the individual strips between Coldham Hall and Rockland Broad, and is incorporated as representing diagrammatically the range of observed relationships of the three chief dominants of the secondary fen areas to each other and to recolonizing woody species.

The presence of *Juncus subnodulosus* as a dominant in the secondary fen areas, while it is practically absent from the primary succession, may be explained if it is regarded as a phase of a deflected succession produced by past economic utilization of the fen. It is not known however whether a Juncetum becomes established in the least well-drained parts as a result of bush clearance alone, or whether intensive summer cutting must accompany such clearance before *Juncus* can become dominant to the taller *Phragmites*. It seems possible that in certain parts edaphic factors may definitely prove limiting in favour of *Juncus*, as in the low-lying parts cleared of 'swamp-carr';

in such cases, it would be expected that the limits of the Juncetum established would be more extensive when regular mowing follows such carr clearance.

The presence of a large area dominated by *Juncus* at the south-west corner of the old Surlingham Broad (see p. 248) may in the same way be interpreted as representing a phase
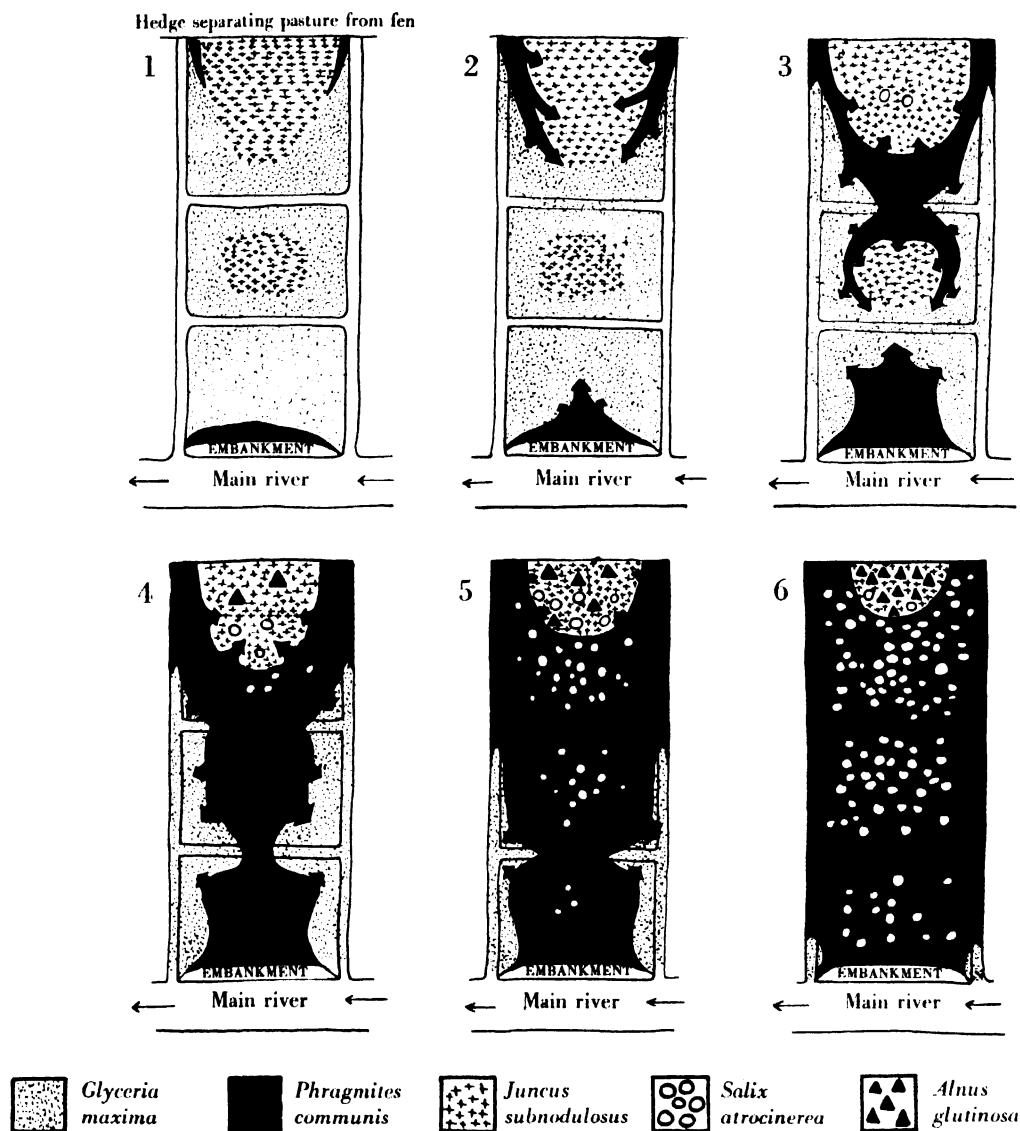

Fig. 10. Diagram showing successive stages in the reversion of cut fen to carr, due to relaxation of cutting and overgrowth of dykes. In the fen strips which are separated from the river by an embankment, as in this diagram, a narrow strip of *Phragmites* was seen to be consistently present immediately behind the embankment. In the other strips, *Glyceria* extended completely to the river bank.

in a deflected succession initiated by past clearing and cutting. The folding map shows that this part is not intersected by drainage dykes, so that there is a relatively large block of peat removed from tidal influence. Cutting has been relaxed for many years, and within the Juncetum re-establishment of young carr—mainly alder—is rapidly taking place. Several patches of mature alder 'swamp-carr' also occur in this area. The

fen zonation from the residual open water of the Broad to this western end is, therefore:

(1) *Primary* Glyceria *hover fen:* too wet and with substrate too unstable for cutting to take place.

(2) *Primary* Phragmites *fen:* in which a little cutting has taken place, but which is becoming colonized by *Salix atrocinerea.*

(3) *Secondary* Juncus subnodulosus *fen:* extensively cut in the past, but now becoming rapidly overgrown with alder bushes, intermixed with some *Salix* in the part nearest the Broad.

The limitation of the Juncetum to the south-west corner rather than to the whole of the western end is the result of the superposition of a second zonation on the first, acting at right angles to it, and developed in relation to the river itself. *Glyceria* is dominant in a strip along the river bank, *Phragmites* occurs farther back, and *Juncus* occupies that part farthest from the river.

In considering the main communities of the secondary fen, some mention should perhaps be made of the position of *Carex acutiformis* Erhr. This species is never prominent in the primary regions, but in the secondary fen it forms fairly extensive societies, though it is not as consistently present as *Juncus, Glyceria* and *Phragmites.* It is most abundant in the more intensively cut areas, and occupies an intermediate position between *Juncus* and *Glyceria* in relation to the tidal dykes; in the latter respect it is comparable to *Phragmites,* and it is noteworthy that it seems to persist as a subsidiary species within the secondary Phragmitetum to a much greater extent than either of the other two.

Cladium mariscus R.Br., which is so abundant in other east Norfolk fens and at Wicken Fen, was here found to dominate only one or two small regions, being especially prominent at the south-west corner of area 28, where it is associated with *Myrica gale* L. The dykes serving this area are completely overgrown, and the fen here has not been cut for many years. It is reported by Mr Ellis that this Cladietum has increased markedly in extent at the expense of the surrounding Juncetum during the last 12 years.

(d) The subsidiary species associated with the chief dominants of the secondary fen

Since the main purpose of the original survey was to plot the distribution of the dominants of the chief communities, it was only possible in the time available to make approximate lists of the subsidiary species associated with them. These lists do not pretend to be complete, but they serve to indicate at least the more constant and prominent of the associates in each case, and an analysis of them is here appended for that purpose. The lists represent the accumulated evidence from five typical societies of each of the main dominants; transitional zones between one community and another are excluded, and the lists do not include those species which were recorded from one area only. The constancy numbers 2–5 are employed in the same way as on p. 245.

The constituent species of the three main communities of the secondary fen
(recolonizing woody species of carr omitted)

	Glycerietum	Phragmitetum	Juncetum
Glyceria maxima (Hartm.) Holmb.	5	.	.
Galium aparine L.	2	.	.
Epilobium hirsutum L.	5	3	.
Urtica dioica L.	5	2	.
Rumex hydrolapathum Huds.	4	3	.
Stachys palustris L.	3	3	.

	Glycerietum	Phragmitetum	Juncetum
Solanum dulcamara L.	3	2	.
Calystegia sepium Br.	2	3	.
Scutellaria galericulata L.	2	2	
Phalaris arundinacea L.	5	2	2
Caltha palustris L.	4	4	5
Angelica sylvestris L.	4	4	5
Phragmites communis Trin.	4	5	2
Lythrum salicaria L.	4	3	4
Eupatorium cannabinum L.	4	3	4
Carex riparia Curtis	4	3	2
Equisetum palustre L.	4	2	2
Peucedanum palustre Moench	4	2	2
Iris pseudacorus L.	3	3	5
Galium palustre L.	3	4	5
Carex paniculata L.	3	4	4
Thalictrum flavum L.	3	3	5
Valeriana officinalis L.	3	3	4
Carex acutiformis Ehrh.	3	3	3
Myosotis palustris Hill	3	2	2
Lysimachia vulgaris L.	2	5	2
Mentha aquatica L.	2	4	4
Vicia cracca L.	2	3	4
Polygonum amphibium f. terrestre Leers	2	2	4
Equisetum limosum L.	2	2	2
Rumex conglomeratus Murr.	2	2	4
Sium erectum Huds.	.	3	2
Carex appropinquata Schum.	.	2	4
Galium uliginosum L.	.	2	4
Carex hudsonii Ar. Benn.	.	2	3
Ranunculus acer L.	.	2	5
R. repens L.	.	2	4
Lychnis flos-cuculi L.	.	2	4
Epilobium parviflorum Schreb.	.	2	1
Cirsium palustre (L.) Scop.	.	2	3
Agrostis stolonifera L.	.	2	2
Dryopteris thelypteris (L.) A. Gray	.	2	2
Calamagrostis canescens (Wigg.) Dr.	.	2	2
Lathyrus palustris L.	.	2	2
L. pratensis L.	.	2	2
Lysimachia nummularia L.	.	2	2
Epilobium palustre L.	.	2	2
Juncus subnodulosus Schrank	.	.	5
Lotus uliginosus Schkurh.	.	.	5
Festuca elatior L.	.	.	4
Scabiosa succisa L.	.	.	3
Holcus lanatus L.	.	.	3
Valeriana dioica L.	.	.	3
Molinia caerulea (L.) Moench	.	.	3
Plantago lanceolata L.	.	.	2
Ranunculus flammula L.	.	.	2
Hypericum quadrangulum L.	.	.	2
Hydrocotyle vulgaris L.	.	.	2
Potentilla erecta (L.) Hampe.	.	.	2
P. anserina L.	.	.	2
Comarum palustre L.	.	.	2
Oenanthe lachenalii C. Gmel.	.	.	2
Centaurea nigra L.	.	.	2
Pulicaria dysenterica (L.) Bernh.	.	.	2
Parnassia palustris L.	.	.	2
Menyanthes trifoliata L.	.	.	2
Rhinanthus crista-galli L.	.	.	2
Carex panicea L.	.	.	2
Briza media L.	.	.	2

Although these lists are necessarily preliminary, nevertheless they serve very well to indicate certain salient points, the most obvious of which is the actual numerical difference in the number of subsidiary species associated with each of the three dominants. The Juncetum carries a far more varied subsidiary flora than the Phragmitetum, and the number of species occurring within the Glycerietum is still more restricted. The relative

abundance of the individual species themselves is not indicated in the lists, but a comparable series was observed in this respect also, the associated species playing a far more prominent role in relation to the dominant within the Juncetum than within either of the other two communities.

It is very probable that the increase in the number and frequencies of the subsidiary species from the Glycerietum to the Juncetum can be more directly related to differences in the growth habit of the dominant than to changes in edaphic and other conditions of the habitat. It has already been shown for the primary fen Glycerietum that early mechanical prostration of the long straggling shoots produces a dense surface mat. The greater stability of the compacted peat of the secondary Glycerieta results in a slightly later prostration of the new spring shoots than in the primary regions, but the fen is so exposed and wind-swept that even here the shoots are beaten down relatively early in the year, and overlie the disintegrating mattress of the dead shoots of the previous year's growth. In areas which were previously mown regularly, the accumulation of litter at the end of the year was cleared annually by winter or early spring burning in order to facilitate subsequent cutting, and the greater number of species recorded from the secondary Glycerieta than from corresponding primary *Glyceria*-dominated fen may probably be as much related to the effect of past burning as to cutting, since in many parts such burning was carried out spasmodically even when the fen was not subsequently cut.

Within the Phragmitetum, the habit of the dominant plant is much more erect, the shoots are less close-set than those of *Glyceria*, and the bare peat can frequently be seen between the shoots on looking down from above even in the complete absence of either burning or cutting. Moreover, even the old dead shoots remain partially or entirely erect at the end of the year; they are brittle, and on decay tend to break up into short lengths, so that they never form the entangled prostrate mass characteristic of *Glyceria* litter. The leaves of *Phragmites* are smaller and less numerous than those of *Glyceria*, and are produced later in the spring, so that there is some opportunity for seeding species to establish themselves before the leaf cover is developed. As the net result of these differences, the Phragmitetum carries a richer subsidiary flora including even the small prostrate *Lysimachia nummularia*, which occasionally occurs in considerable abundance in even dense Phragmiteta.

Juncus subnodulosus has a much lower growth habit than either of the other two dominants, and the erect monophyllous shoots give minimum shading, so that this community is marked by a subsidiary flora which includes many relatively low-growing herbs. The lists show that whereas the Juncetum carries a great many species which are absent from typical Phragmiteta and Glycerieta, there are relatively few species which occur within the two latter but which are absent from Junceta.

The same general difference between the three communities is reflected in a consideration of carr re-establishment. In areas which are known to have been left uncut for many years, as in areas 18–21, the greatest number of young bushes were found within the Junceta (with *Alnus glutinosa* prominent, admixed with *Salix atrocinerea* and a little *Viburnum opulus*); the Phragmiteta carried somewhat fewer bushes (mainly *Salix atrocinerea*), while within the Glycerieta, very few signs of bush colonization could be found. It may be seen from the folding map that throughout the area as a whole very few bushes occur within any of the Glycerieta, and it is suggested that invasion of the

secondary Glycerieta by *Phragmites*, encroaching vegetatively, is a necessary prelude to the re-establishment of carr on such areas.

A direct comparison might well be made with a similar succession preceding bush colonization already noted for the primary regions (see p. 247). In making such comparison, it must be remembered that in the primary regions differences in water level and peat consolidation must be taken into account as possibly directly affecting bush growth; in the secondary fen communities situated on compacted peat, however, these differences do not exist between the Glycerieta and Phragmiteta, and the degree to which carr colonization takes place within them can be related with more assurance to differences in the growth habit of the dominants affecting seedling establishment of the invading bushes.

Apart from the references to the position of *Carex acutiformis* and to *Cladium mariscus*, little has yet been said of other of the more abundant fen species which may in parts become sufficiently prominent to form small societies within the limits of the main communities.

Within the Glycerietum, the most abundant subsidiary species is *Phalaris arundinacea*, but though this forms small scattered societies, it rarely holds a dominant or co-dominant position over any extensive area. *Urtica dioica*, which is generally distributed throughout the Glycerieta, sometimes forms dense beds in those parts which are slightly raised above the general level of the fen, as on the ridges marking the originally excavated peat and subsequent dredgings of some of the dykes (see p. 252). A similar position is occupied by *Epilobium hirsutum*, but in contrast to *Urtica*, this latter species also becomes abundant in parts within the Phragmiteta. *Typha latifolia*, the most abundant and constantly present associate of the primary Glycerieta, is absent altogether from the secondary areas.

The most conspicuous associate of *Phragmites* is *Lysimachia vulgaris*, but although scattered abundantly within the Phragmiteta, it rarely attains a position of dominance in any one part. *Molinia caerulea* and *Filipendula ulmaria* become prominent in the Juncetum, with *Festuca elatior* and *Mentha aquatica* also abundant in parts.

(3) *The relationships of the mowing marsh communities with those of the prisere*

A scheme which embodies the tentative conclusions so far reached as to the successional relationships of the main plant communities within the Surlingham-Rockland peat basin is given in Fig. 11; the main points embodied here have already been dealt with in preceding pages, and no further elaboration is needed at this stage. This scheme is at present in outline only, and it is probable that with further investigation, many of the subsidiary species will be found to have a more important and characteristic role in the fen succession than is at present assigned to them. Apart from the three main fen dominants, *Phalaris arundinacea* and *Carex acutiformis* have also been interpolated in the general plan, but these species are enclosed in rectangles to indicate that they are less generally represented than the other species, being often absent altogether from their characteristic positions.

The chief subsidiary species of the main communities are only given when these are regarded as forming small but especially well-marked subsidiary societies within the general limits of the main dominants themselves. They are incorporated in square brackets beneath the name of the dominant of the main community.
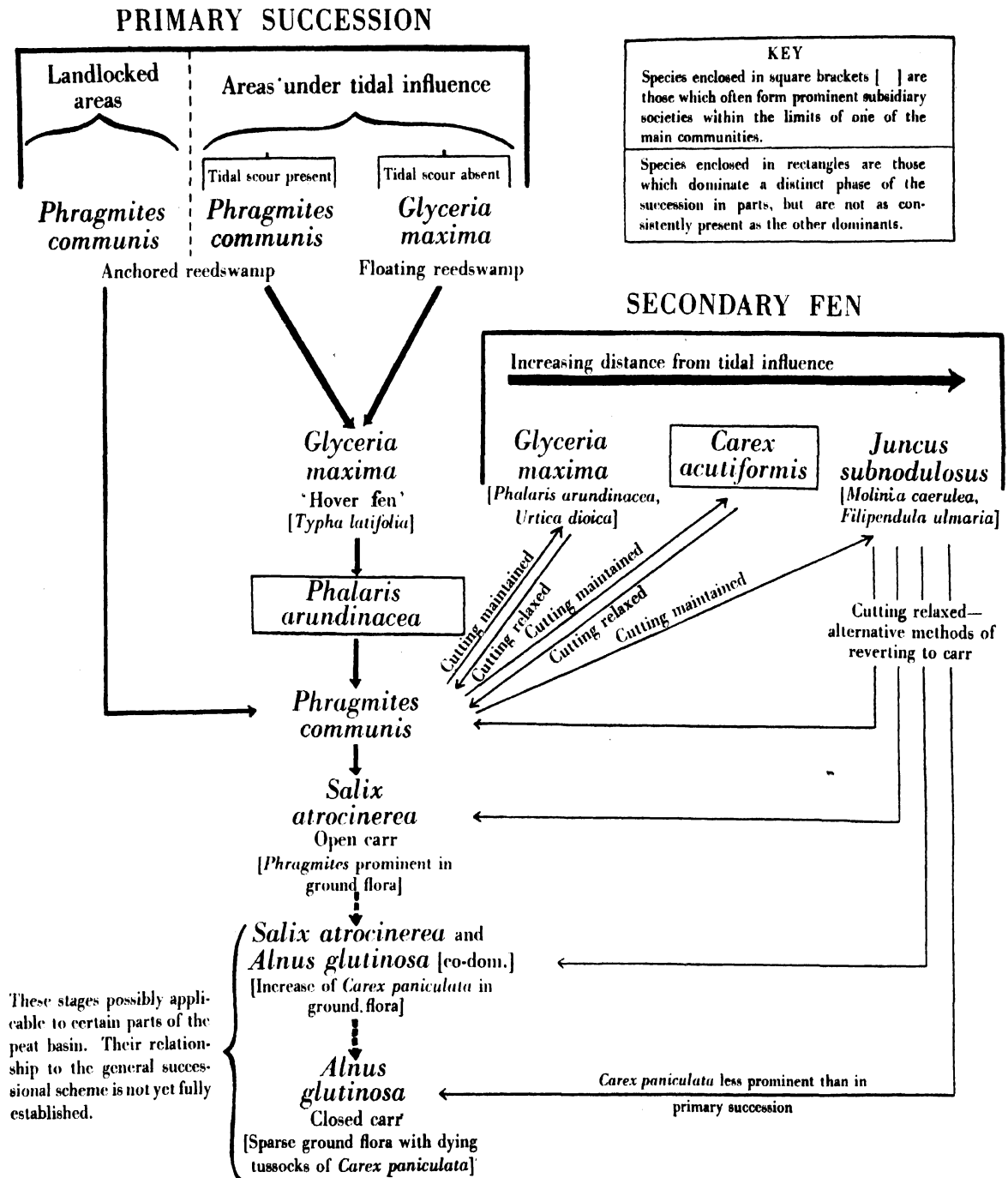
PRIMARY SUCCESSION

Landlocked areas	Areas under tidal influence

KEY

Species enclosed in square brackets [ ] are those which often form prominent subsidiary societies within the limits of one of the main communities.

Species enclosed in rectangles are those which dominate a distinct phase of the succession in parts, but are not as consistently present as the other dominants.

| Tidal scour present | Tidal scour absent |

Phragmites communis

Phragmites communis

Glyceria maxima

Anchored reedswamp

Floating reedswamp

SECONDARY FEN

Increasing distance from tidal influence

Glyceria maxima
'Hover fen'
[*Typha latifolia*]

Glyceria maxima
[*Phalaris arundinacea,
Urtica dioica*]

Carex acutiformis

Juncus subnodulosus
[*Molinia caerulea,
Filipendula ulmaria*]

Phalaris arundinacea

Cutting maintained
Cutting relaxed
Cutting maintained
Cutting relaxed
Cutting maintained

Cutting relaxed—
alternative methods of
reverting to carr

Phragmites communis

Salix atrocinerea
Open carr
[*Phragmites* prominent in ground flora]

These stages possibly applicable to certain parts of the peat basin. Their relationship to the general successional scheme is not yet fully established.

Salix atrocinerea and *Alnus glutinosa* [co-dom.]
[Increase of *Carex paniculata* in ground flora]

Alnus glutinosa
Closed carr
[Sparse ground flora with dying tussocks of *Carex paniculata*]

Carex paniculata less prominent than in primary succession

Fig. 11. The interrelationships of the chief dominants of the primary and secondary areas (excluding grazed areas).

E. DISCUSSION

From the preceding pages, it is clear that the whole area is at present in a condition of vegetational instability, some parts still being at a stage of primary development, while others are entering upon a phase of secondary readjustment following comparatively recent changes in anthropogenic factors of the habitat. Within the latter category may be included both the increasing relaxation of annual cutting over the whole area, and changes in drainage conditions due to overgrowth and neglect of the dykes. The general tendency seems to be towards an initial replacement of much of the *Glyceria* by *Phragmites* preliminary to the re-establishment of carr.

The dependence of *Glyceria* upon the proximity of moving tidal water for its maintenance within the peat basin has been amply illustrated, but so far no suggestion has been put forward as to the physiological basis for such dependence. Comparatively little is yet known as to the general requirements of this species, and in the absence of more specific data, the following translation from Klapp (1937)* might be taken as representative of the main generalizations which the literature so far consulted has provided. Klapp (pp. 152–3) states that: 'This grass prefers localities that are regularly flooded, with a sinking of the water table below the surface in the summer; it also likes canals with slowly flowing, good, not acid water, and finally wet banks.... A prerequisite is an abundance of nutrients in the flood water, and adequate air movement. Acid high moor waters are avoided.'

In a consideration of Klapp's suggestion that the two main factors favouring *Glyceria* are adequate air movement and mineral supply, some attempt is made to estimate the relative dependence of *Glyceria* upon these two factors within the area under consideration. As regards aeration of the substrate, it is true that within the secondary fen areas, *Glyceria* is confined to those parts bordering the dykes which are better drained and where there is probably some diurnal rise and fall of the water table with the ebb and flow of the tide. That oxidizing conditions exist here in the upper layers for at least part of the summer has already been shown by the positive reaction obtained from diphenylamine tests (see p. 254). In contrast to this, however, it may be noted that within the primary areas, the substrata of the Glycerieta show strongly reducing properties, indicated by the strong smell of hydrogen sulphide given off when the underlying peat is disturbed and by the negative reaction of such diphenylamine tests as were made. The fact that in these regions *Glyceria* itself is the primary peat-forming plant also indicates that here it is existing under reducing conditions such as favour peat formation.

It seems more probable that the dependence of *Glyceria* upon the tidal movement of the water is more specifically related to silting and to the renewal of mineral salt supply. In its general distribution, *Glyceria* is far more typical of wet alluvial areas with rich inorganic substrates than of peat regions, i.e. it is a 'marsh' rather than a 'fen' plant. Whereas in the former regions the supply of mineral salts is obtained from the substrate itself, the substrate of peat regions is deficient in nutrients except in as far as they are supplied by the flooding water. Moreover, as has been pointed out by Steffen (1931, p. 115), such mineral salts as are absorbed by peat-forming plants remain locked up in the plant

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* This translation was made by the Imperial Bureau of Pastures and Forage Crops, Aberystwyth, to whom I am much indebted for considerable help with abstracts and translations of Continental references.

remains; they are thus made unavailable to succeeding generations, necessitating a constant new supply from external sources.

It is suggested therefore, as a working hypothesis, that the physiological importance of the considerable tidal movement in maintaining *Glyceria* as a dominant plant of the Yare valley fens (in contrast to its absence from the main fen regions of the other east Norfolk river valleys, where there is less water movement) may prove with further investigation to operate mainly in relation to increased mineral supply. A very significant point in this connexion lies in the fact that, within the Surlingham-Rockland regions surveyed, *the restriction of* Glyceria *to areas supplied by moving tidal water was observed to be applicable only to the peat basin itself; in the surrounding inorganic regions the dykes, ponds, and low-lying water-logged areas were frequently dominated by* Glyceria *even though such dykes had no connexion at all with the tidal system and there was no apparent water movement within them.*

F. Summary of conclusions regarding the distribution, status and relationships of *Glyceria maxima* within the area

1. *Glyceria* forms an integral part of the primary succession from all sheltered open water areas which are under the influence of moving tidal water.

2. It exists in such areas under conditions which are conducive to the formation of fen peat, and is itself the main peat-forming plant in the early stages of the succession.

3. The primary Glycerietum consists of a floating reedswamp which merges gradually into a semi-floating fen with increased peat deposition beneath the mat. The entirely free-floating habit of the *Glyceria* reedswamp is thought to be the direct result of a certain combination of mechanical factors of the habitat related to the specific growth habit of the plant itself.

4. In regions where tidal scour is appreciable, the outer edge of the floating Glycerietum is replaced by a narrow fringe of anchored *Phragmites* reedswamp. This is thought to be maintained against *Glyceria* in this position by purely mechanical factors of the habitat.

5. *Glyceria* is followed in the primary succession by *Phragmites* encroaching from behind by vegetative means. This fen Phragmitetum has no organic connexion with the *Phragmites* reedswamp fringe, and in this case it owes its replacement of *Glyceria* to physiological rather than to mechanical factors.

6. *Glyceria* is absent from land-locked pools within the peat basin, being replaced entirely by *Phragmites* in such parts.

7. The Glycerietum of the primary tidal regions is regarded as an interpolated phase in the succession, occupying part of a zone which in areas with no tidal movement would be dominated throughout by *Phragmites*.

8. In addition to its position in the primary regions, *Glyceria* also forms a prominent constituent of the secondary anthropogenic fen areas, where fen has been maintained in parts which would normally be occupied by carr. The distribution of *Glyceria* in these secondary areas depends upon the drainage conditions obtaining and upon the past history of such areas as regards intensity of annual cutting. Its dominance is favoured by regular summer cutting and by an 'open-dyke' system of drainage which permits free circulation of tidal water between the peat strips.

9. *Glyceria* forms the main agent in the overgrowth of the drainage dykes consequent upon neglect. Its relationship to *Phragmites* in successive stages of dyke overgrowth

Phot. 1. *A small detached portion of* Glyceria *hover drifting with the tide up the main river.* Isolated floating portions similar in size to this are very commonly seen, and may pass and repass the same place many times before finally becoming lodged.

Phot. 2. *A large detached floating 'island' of* Glyceria *hover in the present Surlingham Broad.* Photographed August 1945. This mass, which had clearly been detached fairly recently from the marginal reedswamp, was drifting quite freely about the Broad with every change in wind and tide. Leaves of associated *Typha latifolia* can be seen protruding above the general level of the *Glyceria* mass.

Phot. 3. *Part of the* Phragmites *fringe bordering the central channel of the old Surlingham Broad, at low tide.* The primary *Glyceria* fen is hidden behind the fringe, but a small detached floating mass of *Glyceria* can be distinguished in front of the reedstools on the right, showing the apparent height difference in the habit of the two species. A dense drifting mass of *Ceratophyllum demersum* and *Lemna* spp. occupies the foreground.

Phot. 4. *A drainage dyke of the 'open-dyke' system almost filled with floating* Glyceria *hover encroaching from the marginal* Glycerietum *of the secondary fen bordering the dyke.* The photograph is taken at low tide, showing well the difference in level between the floating hover and the stable fen Glycerietum, although the two are organically connected. At high tide the floating hover rises almost to the level of the fen.

reproduces exactly the relationship between the two observed in the main primary regions.

10. The limitation of *Glyceria* within the peat basin to areas under the influence of moving tidal water is thought to be more probably related to mineral salt supply than to possible aeration of the substrate consequent upon such water movement. This view is supported by the observation that in *inorganic* areas beyond the peat basin, *Glyceria* is frequently dominant in dykes, ponds, and low-lying areas which have no connexion with the tidal system and in which water movement is at a minimum.

11. Both primary and secondary fen Glycerieta contain relatively few subsidiary species in comparison with the other fen communities. It is suggested that the early mechanical prostration of the long *Glyceria* shoots produces a mattress which is effective in preventing the invasion of seeding species and of species of low habit reproducing vegetatively. The same factor appears to be responsible for the fact that within both primary and secondary areas, an invasion of the Glycerietum by *Phragmites* is apparently always a prelude to the establishment of carr.

In conclusion, I should like to express my great appreciation of the encouragement given by Dr E. M. Delf, of Westfield College, during the preparation of this paper.

REFERENCES

Curtis, W. (1777). *Flora Londiniensis*, 1. London.

Deakin, R. (1871). *The Flowering Plants of Tunbridge Wells and Neighbourhood.*

Ellis, E. A. (1934). Wheatfen Broad, Surlingham. *Trans. Norf. Norw. Nat. Soc.* **13.**

Ellis, E. A. (1943). Chloride of some Norfolk waters. Unpubl. notes.

Godwin, H. (1929a). The 'sedge' and 'litter' of Wicken Fen. *J. Ecol.* **17.**

Godwin, H. (1929b). The subclimax and deflected succession. *J. Ecol.* **17.**

Godwin, H. & Tansley, A. G. (1929c). The vegetation of Wicken Fen. *The Natural History of Wicken Fen,* pt. v.

Godwin, H. (1941). Studies in the ecology of Wicken Fen. IV. Crop-taking experiments. *J. Ecol.* **29.**

Godwin, H. & Bharucha, F. R. (1932). Studies in the ecology of Wicken Fen. II. The fen water table and its control of plant communities. *J. Ecol.* **20.**

Godwin, H. & Turner, J. S. (1933). Soil acidity in relation to vegetational succession in Calthorpe Broad, Norfolk. *J. Ecol.* **21.**

Klapp, E. (1937). *Taschenbuch der Gräser.* Berlin.

Laurie, E. M. O. (1944). *Myocastor coypus* in Gt Britain. Unpubl. notes.

Lecoq, H. (1844). *Traité des plantes fourragères.* Paris.

Pallis, M. (1911). The river valleys of East Norfolk. Chap x in *Types of British Vegetation*, ed. Tansley, A. G.

Pallis, M. (1915). The structure and history of Plav: the floating fen of the delta of the Danube. *J. Linn. Soc. (Bot.),* **43.**

Pearsall, W. H. & Mortimer, C. H. (1939). Oxidation-reduction potentials in waterlogged soils, natural waters, and muds. *J. Ecol.* **29.**

Richards, P. W. & Clapham, A. R. (1941). *Juncus subnodulosus* Schrank. In Biological Flora of the British Isles. *J. Ecol.* **29.**

Steffen, H. (1931). Vegetationskunde von Ostpreussen. *Pflanzensociologie,* **1.**

Tansley, A. G. (1939). *The British Islands and their Vegetation.* Camb. Univ. Press.

STUDIES IN THE ECOLOGY OF RIVERS

VI. THE ALGAL GROWTH IN CERTAIN HIGHLY CALCAREOUS STREAMS

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(*With four Figures in the Text*)

INTRODUCTION

It was recorded in a previous paper (Butcher, 1938) that contrary to the results obtained on the rivers Tees (Butcher, Longwell & Pentelow, 1931), Lark (Butcher, Pentelow & Woodley, 1937) and Bristol Avon (Pentelow, Butcher & Grindley, 1938) the algal growths on the river Hull (a canalized stream) showed no very definite seasonal variation in species and very little in quantity. The collections were taken at comparatively long intervals, and it was thought possible that some sudden increases of certain algae may have been missed. While stationed at Alresford, Hampshire, opportunity was therefore taken to make more frequent counts of the algae growing in the river Itchen at that place together with supplementary collections at other places on that stream and on the neighbouring Test, a river of similar character to the Itchen. The general character of the Itchen was described by Butcher (1927) and the method of collecting (Butcher, 1940).

For a period of 12 months counts were made of the algae growing on glass slides that had been on the river bed for 5, 10, 20, and 30 days respectively, and these counts were made at intervals of 10 days, making a total of about 150 counts. It seems most unlikely that with such frequent observations any important variations could have been missed. During the following 6 months the time of immersion of the slides was increased to give 30-, 40-, 50- and 60-day counts in order to get some idea of the point where equilibrium between increment of growth and loss due to changing physical conditions was obtained.

In addition to the series laid in the river where the average current was 3000 m./hr., a set was put in a small pond 15 ft. × 9 ft. × 18 in. which was being fed from the river by a channel 120 ft. long and so had water of the same composition, presumably, as the river. The samples are referred to as the pond samples. Other series of collections at intervals of 20 days were taken at St Cross and Woodmill, 7 and 16 miles respectively downstream from Alresford, and at Longstock on the river Test.

The method of obtaining the necessary data at Alresford was as follows. Two frames, each containing four slides, were laid side by side in pond or river. From one, the up-river slide was removed every 5 days and nos. 2 and 3 or 2 and 4 alternatively at intervals of 10 days. This gave the 5-, 10- and 20-day series. In the other frame one slide was removed at intervals of 10 days, nos. 3 and 4 being removed together. This gave the 30-day series with no. 4 a duplicate. For the 20–60-day series four frames each with five slides were used, fixed side by side. One frame was devoted entirely to the 50-day series, a second to the 60-day series, a third to the 40-day series, with the bottom slide for the necessary 60-day otherwise missing, while from the fourth frame the order of removal of the slides was up-river (no. 1) and bottom 2 and 4, 1 and 3, 2 and 5, 1 and 4, 2 and 3, thus giving the 20- and 30-day series.

It was possible to do most of the counting under a $\frac{1}{10}$th water immersion lens aided by an eyepiece micrometer limiting an area of 0·0225 sq.mm. Fifteen or twenty fields were usually counted taken diagonally across the slide at intervals of 0·5 cm. More were counted when the growth was very thin. When the growth was thick (more than about 9000 organisms/sq.mm.), it had to be scraped off and diluted with water, shaken and the contents of $\frac{1}{10}$ ml. spread on a ruled slide and counted. In this quantity there were usually about 2000 organisms.

The data presented in the tables may be used to show three things. Each column read vertically shows seasonal change with a constant time of immersion. In Table 1 read horizontally, or Table 3 read diagonally, the figures give algal flora on the day of collecting
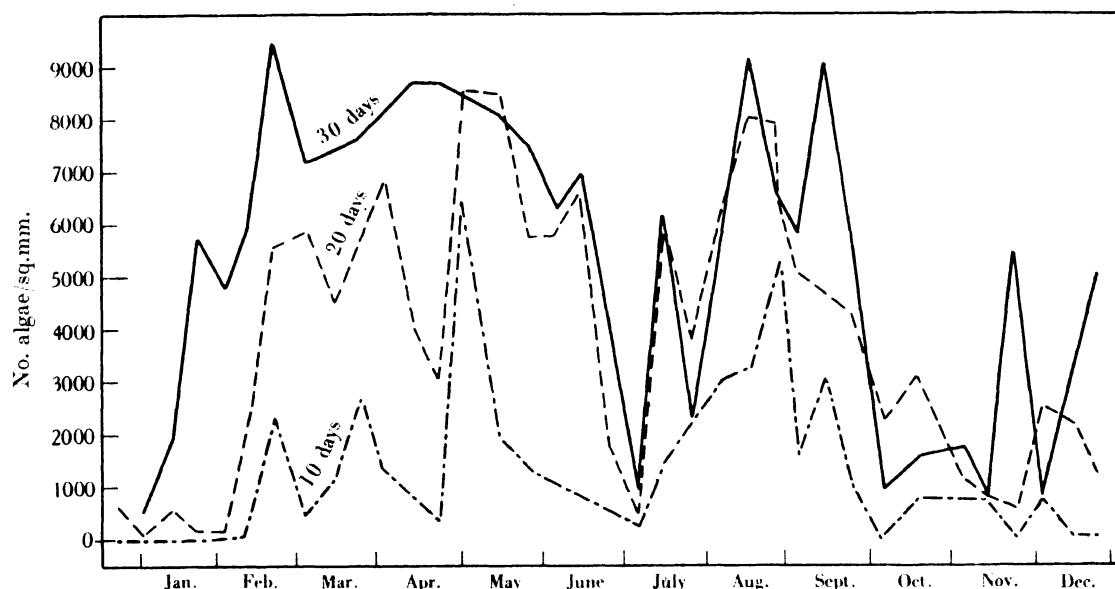

Fig. 1. Total growth of algae/sq.mm. in the river Itchen at Alresford for periods of submergence of 10, 20 and 30 days. Jan.–Dec. 1935.

and on slides which have been immersed for various periods. In these same tables the figures read diagonally (Tables 1 and 3) or horizontally (Tables 7 and 8) give the details of colonization and change in a given batch of slides immersed for the same day. Only the average figures of the more important algae are usually given, but the whole data may be examined on application to the author.

TOTAL QUANTITY OF ALGAE

A graph of the total amount of the growth for the river Itchen appears in Fig. 1. It comprises a series of irregular curves from which it is not easy to decide whether there is a seasonal periodicity or not. From the 30-day curve one might postulate periods of maximum development from February to June and from August to October, but this is not supported by the 30-day pond curve (Fig. 2), where the maxima are July and September, and only in part by the 20- and 10-day curves. In the 20–60-day results (Table 1) only irregular fluctuations can be detected. The curves of quantity therefore correspond on the whole to those obtained on the river Hull (Butcher, 1938) and are formed of a single annual cycle with maximum about midsummer and minimum in winter.

Table 1. *Quantities of algae in nos./sq.mm. growing in the river Itchen and the pond at Alresford*

Days submerged ...	River					Pond				
Date collected	20	30	40	50	60	20	30	40	50	60
15. ii. 36	5819	8908	4482	14206	7577	1608	1630	5621	5897	5106
9. iii. 36	4005	7271	5913	6403	7535	2574	6114	4285	5751	7710
21. iii. 36	5738	—	5151	6049	7338	4446	—	3411	4541	9471
3. iv. 36	3330	5780	—	6633	4415	5427	5359	—	2630	2858
14. iv. 36	5998	6569	4379	6877	6260	2274	1254	2051	1048	4549
26. iv. 36	4471	2475	5620	5250	5536	1350	830	1150	1421	2242
8. v. 36	5688	5102	5773	5306	4961	862	1284	1973	1271	2712
18. v. 36	4961	6606	6363	8569	7232	1603	1103	1847	1965	2598
30. v. 36	4568	5709	3051	4534	3671	2744	2063	2025	1344	1433
14. vi. 36	4409	7660	9283	4226	15969	808	1813	1450	1284	1160
Means	4709	6230	5535	6806	6949	2390	2383	2646	2715	3944

For progress of colonization read diagonally downwards to right.
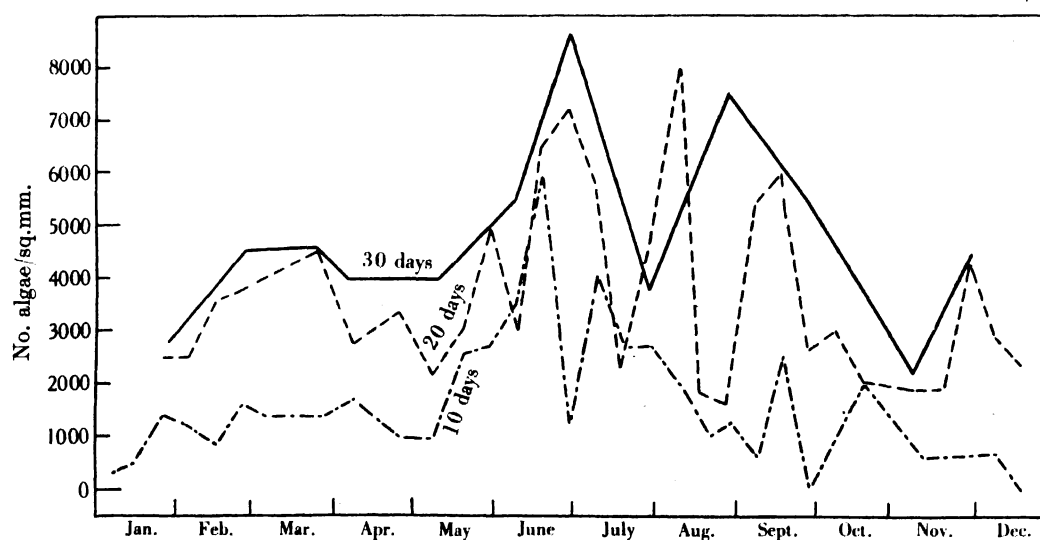

Fig. 2. Total growth of algae/sq.mm. in the pond at Alresford Experimental Station for periods of submergence of 10, 20 and 30 days. Jan.–Dec. 1935.

On this general curve are superimposed irregular fluctuations probably caused by quickly changing external physical factors such as floods, turbidity and sunlight as well as by strictly local biological and physical events such as the browsing of animals on the growth, the complete detachment of a film due to the formation of gas bubbles, and the rubbing away of algae by foreign bodies moved by the current. It should be noted also that if one had taken single monthly collections, i.e. every third point on the graph, the curve would have been much smoother, and the low point at the end of July either would not be shown at all or, if it had been the July collection, it would have assumed great significance and divided the annual cycle into two periods of maximum growth (cf. also the curves in Fig. 3, which are at 30- or 20-day intervals).

The general curve on which all the smaller fluctuations are apparently superimposed is clearly distinguishable in the results from other stations in the Itchen, Test and Hampshire
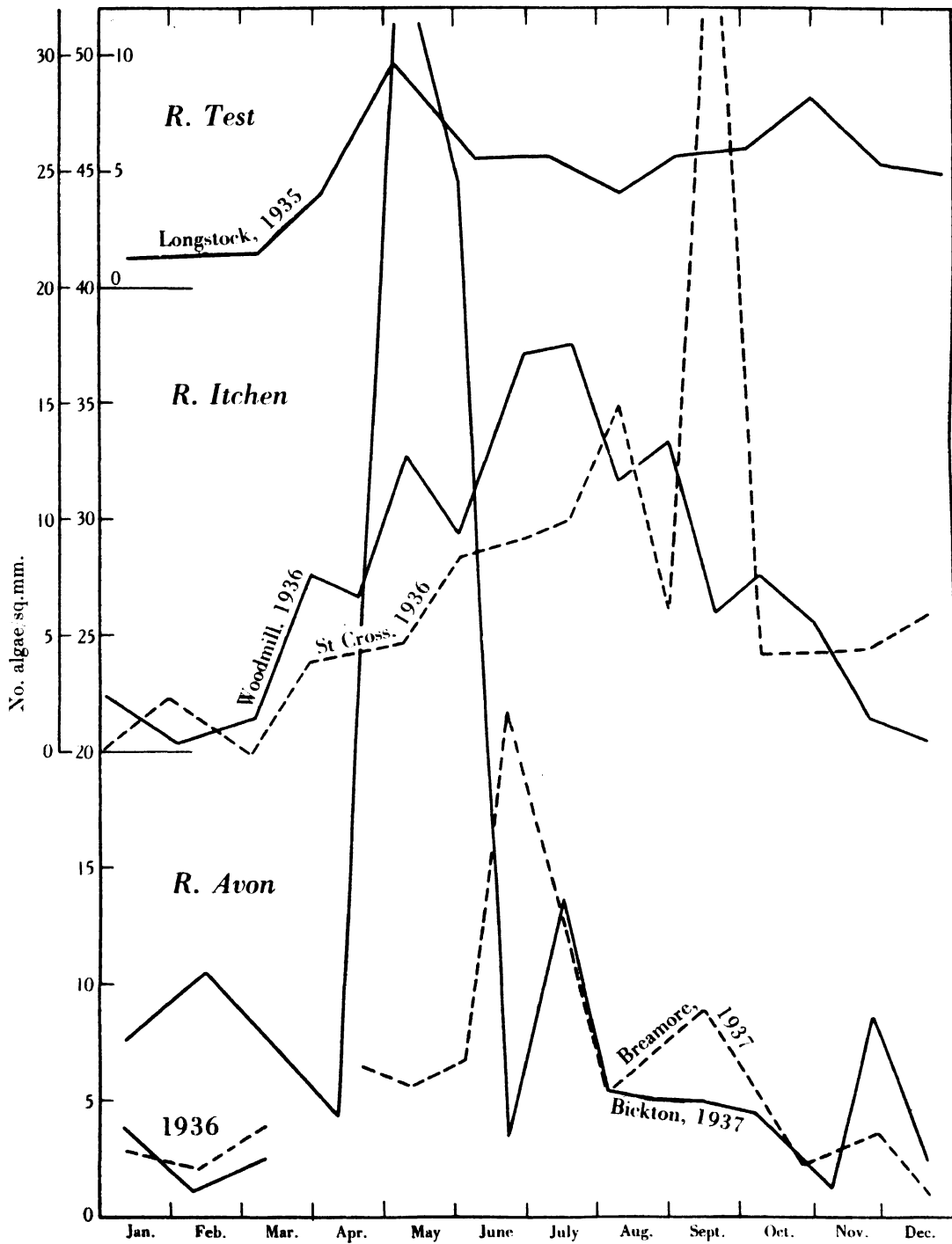
Fig. 3. Total growth of algae/sq.mm. in the river Test at Longstock (Jan.–Dec. 1934), the river Itchen at St Cross and Woodmill (Jan.–Dec. 1936) and the Hampshire Avon at Breamore and Bickton (Jan. 1937–Mar. 1938).

Avon; minimum amounts are found between December and February, a steep rise in March to May, irregular fluctuations throughout the summer, and a gradual fall to minimum values in December. It is natural to assume that this variation is an annual one caused by some slowly and constantly changing physical factor such as the length of daylight or temperature, but on this point the data are confusing and insufficient. Both Pearsall (1923) and Butcher, Longwell & Pentelow (1931) quote figures which show no relation between diatom maxima and temperatures, and in the results from almost all rivers examined the maximum period of growth, May to July, comes well before the season of highest water temperatures (July to August).

Table 2 below gives the quantity of algal growth at Alresford and the total sunshine for the previous 5–10 days at Long Sutton, about 10 miles away. Here again little corre-

Table 2. *Quantities of algae in nos./sq.mm. growing in the river Itchen at Alresford on slides after 20 days (and 5 days) and sunshine, rain and air temperatures*

	No. of algae/sq.mm.				Previous* 5 days' rainfall in in.	Previous* 5 days' sunshine hr.	Mean temp. ° F.
Date	River 20 days	Pond 20 days	River 5 days	Pond 5 days	Ovington	Long Sutton	Alresford
1. ii. 35	49	48	62	74	0·09	16·7	43
12. ii. 35	616	712	356	150	0·04	16·1	33
22. ii. 35	203	1335	11	248	1·13	9·2	—
3. iii. 35	236	2522	43	308	1·09	13·8	32
13. iii. 35	2729	2578	34	366	0·19	16·5	33
23. iii. 35	5653	3620	379	813	0·13	30·8	47
2. iv. 35	5929	3882	93	818	0·00	15·9	47
17. iv. 35	4543	—	60	459	1·06	27·8	43
24. iv. 35	5660	4602	1011	977	0·99	19·6	48
4. v. 35	6858	2824	573	895	0·24	25·2	49
14. v. 35	4118	3918	1100	565	0·06	42·4	54
25. v. 35	2942	—	—	1439	0·07	34·7	51
4. vi. 35	8652	3331	2602	1099	0·12	25·8	57
15. vi. 35	8568	2260	1102	550	1·60	23·6	55
25. vi. 35	5871	3088	570	848	0·05	33·7	64
5. vii. 35	5813	5092	1880	1100	0·68	27·2	61
15. vii. 35	7010	3071	1266	907	0·00	50·7	68
25. vii. 35	1788	6512	3703	3415	0·36	28·1	57
4. viii. 35	414	7303	—	—	0·00	41·7	60
14. viii. 35	6248	5864	515	976	0·06	40·9	59
25. viii. 35	2244	2440	324	689	0·58	38·4	60
4. ix. 35	5259	4627	824	2231	1·11	17·3	60
16. ix. 35	9207	8222	728	2102	0·51	29·5	57
26. ix. 35	6639	1805	930	849	0·01	26·7	58
6. x. 35	5816	1780	201	491	2·21	16·1	49
16. x. 35	9178	5497	248	461	0·00	18·3	53
26. x. 35	5594	6012	64	1101	0·58	22·5	40
5. xi. 35	956	2742	13	27	0·03	5·2	36
18. xi. 35	1625	2996	521	1334	0·17	7·7	36
5. xii. 35	1841	233	—	—	1·63	11·5	48
15. xii. 35	759	—	28	248	2·09	0·7	43
24. xii. 35	589	1896	2	—	0·65	12·7	35

lation can be seen, and the same may be said about the relationship of sunshine and algal growths on the Test and the lower Itchen. On the other hand, the number of algae appearing in 5 days is almost always larger when the amount of sunshine is high, suggesting that sunshine, though not a predominant cause, does induce more rapid growth of the algae. July is often a month with little sunshine and also low amounts of algae, and it was at first thought these might show some correlation (as, indeed, they do in 1937),

* By courtesy of the Meteorological Office, Air Ministry.

but in 1935 maximum sunshine came in July, and some of the curves of the algal growth showed the usual decrease in that month.

The cause of the smaller fluctuations is equally obscure. The factors usually invoked are rainfall and food substances dissolved in the water. Rainfall may react in three ways: by increasing the turbidity of the water and hence cutting down the light, by causing greatly increased current speeds which scour away the algae, and by washing into the river increased amounts of dissolved salts. Fed by springs and situated on the upper chalk, the Itchen at Alresford maintains a level constant to a few inches throughout the year, and turbidity and water level change only after exceptionally heavy rainfall, so flood and turbidity may here be ruled out as causal factors in the algal growth. Also there does not appear to be any relationship between algal growth and the preceding 5 days' rainfall shown in Table 2.

The Itchen is rich in calcium (hardness 18 pt. $CaCO_3/100,000$) and contains a plentiful supply of dissolved salts compared to, say, the English lakes, and it seems unlikely that any of these salts ever becomes a limiting factor. Of the strictly local factors mentioned above which cause sudden decreases, the browsing of animals is the most important. The relationship of the animal to its algal food is a very important one which has as yet hardly been touched upon, and it can only be mentioned here as yet another factor producing variations in the amount of algal growth.

The disappearance of growths due to the formation of gas bubbles underneath the film and the rubbing away of algae by odd bits of debris are even more irregular and local and consequently the minima they cause in exceptional circumstances can be very misleading when the data are few, and given proper place only when the data are sufficiently numerous.

It is clear from the above considerations that there are a large number of factors which at a given time and place can influence algal growth and cause fluctuations of greater or less intensity, usually locally in one portion of a river bed, but sometimes over considerable distances. These are well seen in the results from the Itchen, and until examined carefully give a false idea of a seasonal curve. The extreme case of a local fluctuation lies between 25 July and 4 August 1935, when, in the river, the growth was reduced in a way best shown in Table 3. The period was sunny and dry with a clear river, and as this

Table 3. *Growth of algae in nos./sq.mm.*

Immersed	After 5 days	After 10 days	After 20 days	After 30 days
5. vii. 35	1765	3171	1788	820
15. vii. 35	322	4808	414	5854
25. vii. 35	3197	369	6248	3805

Figures read diagonally upwards to right show the quantities on a given day.

marked decrease is not shown in the pond samples over the same period, it is clearly an example of variation due to a factor local to the river. Nothing abnormal was noted at the time, so the cause is still to be discovered.

COLONIZATION

In a general way colonization of the glass slides appears to be completed in about 20 days except in the winter, when growth is evidently slow and colonization takes 30–40 days, a fact clearly brought out in the 30–60-day series (Table 1). In slides left for periods

between 30 and 60 days both negative and positive increments are shown. Many of these are within the limits of experimental error which for this method of counting has been calculated as a mean deviation of $\pm 50\%$, but there are some cases which show an actual loss of algae and a change in the nature of the growth as between 20 and 30 or between 30 and 40 days (see later). In the pond, where growth is apparently slower and the quantities of algae not so large, it is axiomatic that colonization will take longer to complete, and here it would appear to be done in 30–40 days. Godward (1934) studied the distribution and colonization of algae on phanerogams in a small pond, and it is clear from her observations that there, also, colonization was simply a matter of the time the substratum had been in the water (young leaves, for example, are immersed a shorter time than the mature ones), together with the rapidity of growth of the algae at the time. It is apparently independent of the nature of the substratum. The figures from the Itchen support these observations.

Both the rivers Test and Itchen are virtually unpolluted, but the water contains a plentiful supply of calcium, other mineral salts and a certain amount of organic plant food. The composition of the water is probably related to the nature of the drainage plane. It is supplied chiefly from springs in the chalk, while surface water, which is only a very small proportion of the rainfall, drains a well-cultivated and manured lowland district. Using the ecological term applied in the classification of lakes, these streams are eutrophic. It is significant, therefore, that the average number of algae is of the same order (2500–10,000/sq.mm.) as found in other eutrophic waters. Judging from data obtained from other rivers the amounts of algal growth appear to fall into four groups, the others being oligotrophic waters with less than 2000/sq.mm. (e.g. the river Tees near its source), polluted or mesosaprobic waters with 10,000–100,000/sq.mm. (e.g. the Bristol Avon), while in the polysaprobic waters (e.g. the river Tame) the numbers again are low. In a similar way in nearly all rivers there is progressive change in the composition of the water as it passes from source to mouth. It becomes richer in salts and organic matter from drainage and this is usually accompanied by an increase in the quantities of algae. To this the Itchen is no exception. The mean values are at Alresford 4709, at St Cross 8349 and at Woodmill 9426 algae/sq.mm. respectively.

Alternatively, since the speed of flow is considerably less at Woodmill than at St Cross or Alresford the increase could be caused by the small current at the first place, but this does not account for the increase at St Cross as compared with Alresford where the currents are almost the same, nor for the lower value for the pond (2390 algae/sq.mm.) as compared to the river. If one can assume that the current of a stream as measured by floats on the surface bears some relation to the microscopic current over the algal film, the data here presented do not support the opinion usually held that algal growth is inversely proportional to the current. In all the rivers here considered where comparisons can be made, the places with vigorous current produce more algae than the places with little current. On the Hampshire Avon (see Table 5) Latchmore has the fastest and Bickton has the slowest current. On the Itchen the order from slow to fast is: pond (above the Alresford weir), Woodmill, St Cross (below the Alresford weir), and the average algal growths/sq.mm. are 3600, 3530, 9426, 8349 and 4700 respectively.

Hence it is not alone the increased current of flood water which reduces algal growth, but rather its scouring action helped by the debris it contains together with the comparative suddenness of the changing current velocities. These facts have an important

bearing on the so-called river plankton. The greatest quantities of free-floating micro-organisms are present immediately after the flood, the source of which are the bottom growths scoured and washed into the water and such maxima are purely temporary. After the scour the numbers are small and then gradually increase with the increasing increment of sessile growths. The increase of plankton on low water and in summer, such as recorded for the Thames by Rice (1938), could be assigned equally well to the greater penetration of light to bottom-living algae and the smaller dilution as to the decrease in current. This matter of current is discussed further on pp. 278-9.

Table 4. *Algae in the river Tees*

Miles from source ...	14	16	20	23	26	29	31	34	36	51	57	67
Achnanthes	1200	1800	1300	3000	600	1800	1600	250	1600	—	—	—
Chaetopeltis	40	10	—	220	20	20	—	—	—	—	—	—
Cocconeis	—	—	20	720	2100	150	900	800	1900	1800	100	900
Ulvella	20	10	—	430	500	350	620	80	450	300	1200	70
Chamaesiphon	—	—	30	—	380	20	1800	300	1400	1700	20	1200

Sewage drains in just above 20, 26, 31 and 51.

THE NATURE OF THE ALGAL COMMUNITIES

Table 5 gives the average numbers of algae taken over a long period in the Itchen, Test and Hampshire Avon. A full list of species as far as they were determined appears in the Appendix. Ignoring the pond for the time being the five dominant species are *Cocconeis placentula, Achnanthes minutissima, Chamaesiphon incrustans, Ch. regularis* and *Ulvella frequens*. Other algae present in some quantity at all places are *Achnanthes lanceolata, Gomphonema parvulum, G. olivaceum, Nitzschia palea* and *Cymbella ventricosa*, all diatoms; the Chaetophorales, *Sphaerobotrys fluviatilis, Protoderma* sp. and *Stigeoclonium farctum*, and the blue-green alga *Phormidium foveolarum*.

Table 5. *Principal species of algae, average nos./sq.mm. in various rivers*

	Pond, Alresford		Itchen				Test, Long-stock	Hampshire Avon, Breamore, Bicton, Latchmore		
			Alresford		St Cross, Woodmill					
Period	20 days Jan. 35– June 36	60 days Feb.– June 36	20 days Jan. 35	60 days Feb.– June 36	June 36–Mar. 38		June 33– Jan. 35	Mar. 36–Mar. 37		
No. of collections...	42	10	42	10	28	28	21	15	15	15
Cocconeis placentula	700	1900	1500	1300	2500	1500	2500	2500	2900	2100
Achnanthes minutissima	1200	—	400	400	1900	2600	500	700	900	2200
A. lanceolata	—	—	—	100	100	200	100	100	300	100
Gomphonema spp.	200	500	100	200	400	600	—	1900	700	1500
Cymbella spp.	—	—	—	—	500	900	100	200	200	100
Nitzschia palea	—	—	100	—	100	500	200	1100	800	4700
Ulvella frequens	400	600	200	200	500	500	200	500	500	700
Sphaerobotrys fluviatilis	—	200	100	200	200	300	—	300	200	800
Stigeoclonium sp.	100	100	—	200	200	500	100	100	200	200
Chamaesiphon spp.	400	400	1400	3900	900	1400	1100	1500	1300	4600
Others	600	300	300	500	400	900	300	2100	2000	1800
Total	3600	4000	4100	7000	7700	9900	5100	11000	10000	18800

Achnanthes minutissima also includes *A. linearis. Gomphonema* includes *G. olivaceum, parvulum* and *constrictum. Cymbella* includes *C. ventricosa, affinis* and *lanceolata. Chamaesiphon* includes *C. incrustans* and *C. regularis*.

With rare exceptions these dominants are present in quantity throughout the year, and though the members fluctuate considerably between themselves, neither a seasonal cycle nor smaller regular variations can be detected (see Fig. 4). This community is identical to that found, either all the year round or as a definite summer community, in a very large number of rivers which have been systematically examined. In the Tees (Butcher *et al.* 1937) it was shown that this community was dominant in the middle and lower reaches throughout the summer, but in the uppermost portions there was an *Achnanthes-Chaetopeltis* community. This was replaced by *Cocconeis-Ulvella* wherever sewage drains flowed into the river in quantity, reappeared if the dilution was great and decomposition rapid, but eventually disappeared altogether. The results of one series of collections taken down the whole river are shown in Table 4. In its uppermost reaches among mountain and moorland the river water is deficient in dissolved salts and organic matter and may be said to be oligotrophic. Passing downstream the river, through drainage of more fertile land and more particularly from human and animal populations, is gradually augmented with organic matter and dissolved salts, a process conveniently known as eutrophication. The above figures of the Tees show the replacement of an oligotrophic community (*Achnanthes-Chaetopeltis*) by one (*Cocconeis-Chamaesiphon*) characteristic of eutrophic waters, a process accelerated where sewage drains in.

The streams now being considered, the Itchen, etc., are all highly calcareous, but the upper Tees is a soft water, 3–5 pts. CaO/100,000, so it is clear that it is not the hardness of the water which determines the presence of this community. Rather may it be considered the climax in an algal succession as all rivers become progressively eutrophicated downstream.

A point of very great importance to this climax community is undoubtedly the absence of a periodicity dependent on the season. The numbers of the various members fluctuate between themselves, but they still remain present in some quantity all the year round. There are sudden increases of other algae illustrated here by *Gomphonema olivaceum* which may have a maximum in the spring but rarely at a definite period (see especially Itchen, Fig. 4 *a*). Where seasonal variation among sessile algae has been recorded in eutrophic streams the above has been the summer community, while the spring community comprises species entirely different from the above and they usually are *Navicula viridula*, *Surirella ovalis* and *Ulothrix zonata*. In the rivers now being considered these are rare species. No reason can at present be given as to why these rivers (Itchen, Test, Hull, Hampshire Avon) show no seasonal variation, while the Bristol Avon (Pentelow *et al.* 1938), Tees, Lark (Butcher *et al.* 1931) and Thames (Rice, 1938) show spring maxima of species different from the summer ones, but it is probably related to the soil and underlying rocks of the district and also to the nature and volume of the drainage and waste waters and the type of flooding.

ALGAL SUCCESSION

Table 6 gives the average quantities over a year and 6 months respectively of the dominant algae growing on glass slides in the Itchen and the pond after 5, 10, 20, 30, 40, 50 and 60 days. The order of frequency and proportion of quantity remain much the same throughout, the only possible exception being the later development of *Chamaesiphon*. This, however, is an addition to and not a replacement in the community. Thus there is no algal succession, a fact which confirms the view that here one has a climax association.
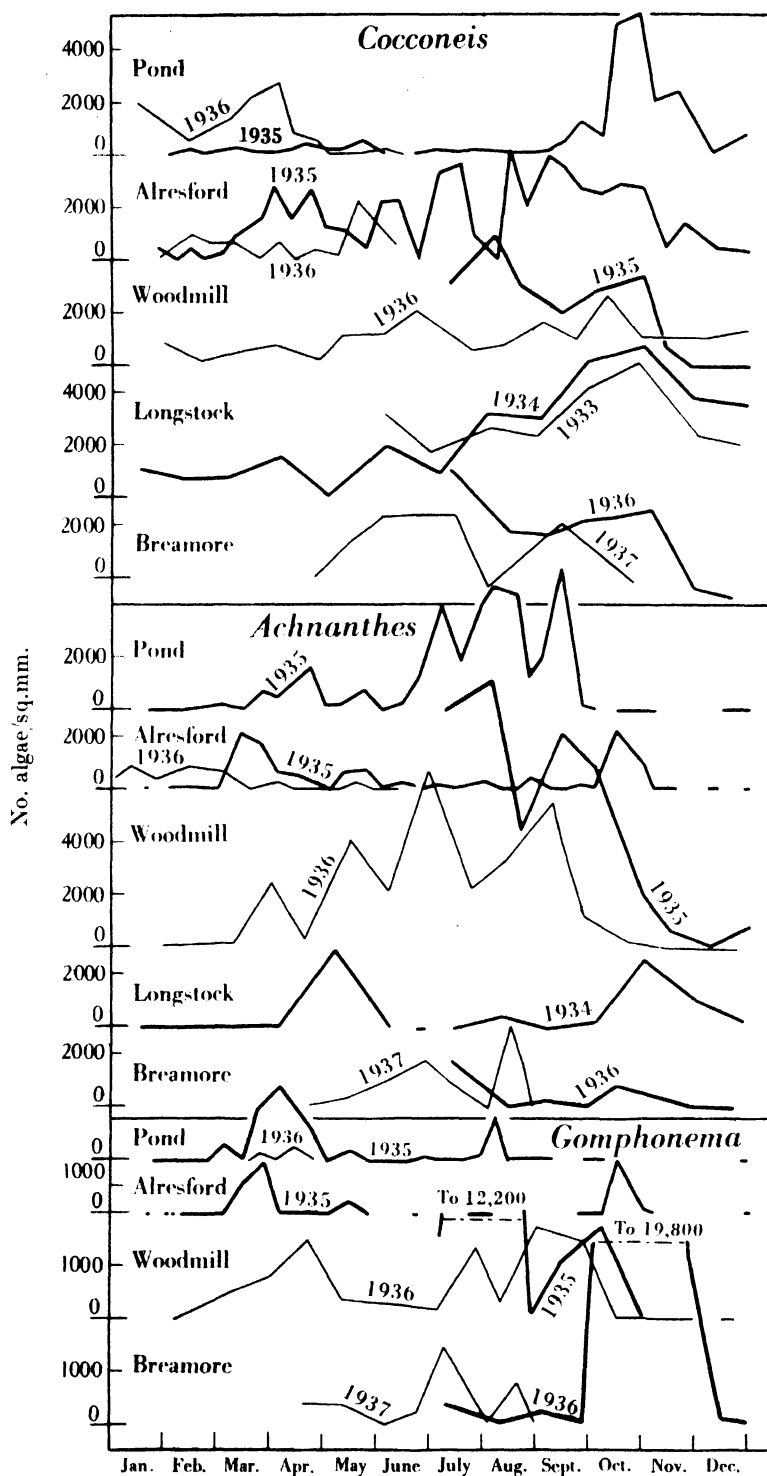
Fig. 4a. Quantities of certain dominant algae/sq.mm. developing in 20 days in the pond and river at Alresford, in the river Itchen at Woodmill, in the river Test at Longstock and the Hampshire Avon at Breamore. Samples taken up every 10 days at Alresford, every 20 days at Woodmill and Breamore and every 30 days at Longstock.

The following algae were not in sufficient quantity to be included: *Achnanthes* in the pond in 1936 and at Longstock in 1933; *Ulvella* in the river at Alresford in 1936 and at Longstock in 1933; *Chamaesiphon* in the pond in 1936; *Gomphonema* in the river at Alresford in 1936 and at Longstock.

Table 6. *Development of algal communities. Annual mean nos./sq.mm. of algae on glass slides submerged for various periods in the river Itchen and a pond at Alresford*

No. of days submerged ...	Feb. 1935–Jan. 1936				Feb.–June 1936				
	5	10	20	30	20	30	40	50	60
			(a) River						
Cocconeis placentula	217	912	1500	1940	800	1520	960	740	1580
Achnanthes spp.	125	304	400	655	150	320	300	220	580
Gomphonema spp.	18	45	100	354	100	110	40	250	160
Ulvella frequens	38	68	200	235	80	210	150	210	320
Chamaesiphon spp.	26	134	1400	1864	4520	4260	1900	3580	4020
			(b) Pond						
Cocconeis placentula	140	334	730	1350	820	1180	1320	1860	1540
Achnanthes spp.	400	539	1150	803	60	140	100	14	10
Gomphonema spp.	30	59	210	455	80	80	60	520	30
Ulvella frequens	160	321	410	491	260	600	1180	700	700
Chamaesiphon spp.	40	86	410	740	100	240	60	320	120

Table 7. *Quantities of* Ulothrix *as no. cells/sq.mm. on glass slides submerged in the river Itchen*

Date submerged	No. of days submerged				
	20	30	40	50	60
4. vi. 36	282	—	—	—	—
18. v. 36	0	1324	—	—	—
8. v. 36	1024	0	617	—	—
26. iv. 36	0	594	0	100	—
14. iv. 36	0	0	188	0	1065
4. iv. 36	—	0	0	453	59
21. iii. 36	—	—	0	0	147

For the progressive change of a given set of slides read horizontally.
For a set of slides collected on the same date read diagonally downwards.

In the apparatus used for this work, five glass slides were fixed in a frame and one only removed every 10 days. The results taken over a period show not only the increment of growth and nature of the community as a whole but also the decrease in the quantity of any species. Although growth is usually a steady increase to about 30 days an organism can suddenly increase within a 10-day period, or what is even more important it can decrease or even be completely washed away and reappear again within a month or so. The most striking case was of a double 'wave' of *Ulothrix aequalis* in May 1936 recorded in Table 7. Naturally the diatoms, being lightly attached to the substratum, react quickly to changing conditions, and this is well shown for *Gomphonema*. *Chamaesiphon* and *Ulvella* do not show so definitely.

DIFFERENCE OF POND AND RIVER

With so little change in the water of pond and river one would have expected a similar algal community to develop in both. The difference between them is one of the most striking facts which has arisen in this work. The species present are much the same, but their numerical proportion is quite different (see Table 6). In the river *Cocconeis* and *Chamaesiphon* as a rule make up 80% of the community; *Achnanthes*, *Gomphonema* and *Nitzschia palea* are frequent, but the Chaetophorales *Ulvella*, *Sphaerobotrys*, *Chaetopeltis orbicularis* and *Stigeoclonium farctum* are in much smaller quantity. In the pond while

Cocconeis still dominates, the Chaetophorales usually occupy the second place, and the diatoms are much fewer though on the whole comprising the same species. Occasionally a series of growths in the pond would be almost indistinguishable from those in the river. Further, in spite of quieter conditions the growth in the pond was slower than that in the river after the first 10 days. The algal community of the Hull canal approximates closely to the pond, and that in the West Beck to the river Itchen.
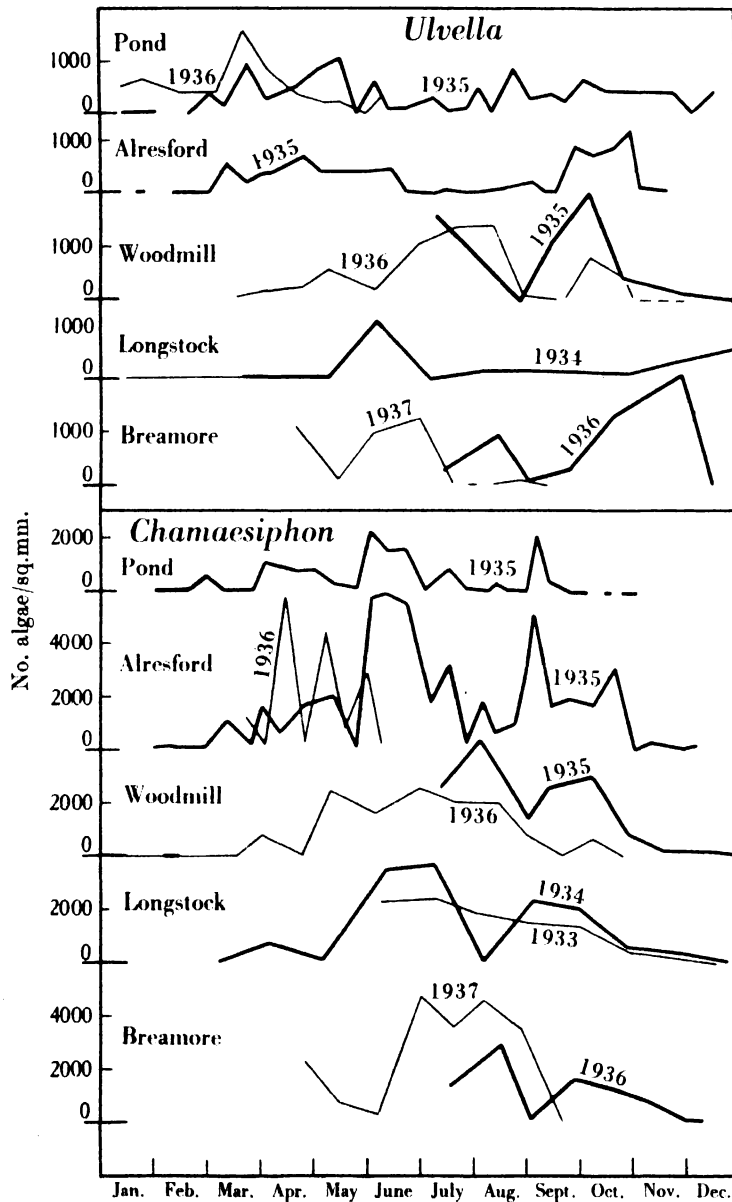
Fig. 4*b*.

It would seem from these results that there is a fundamental difference between still and running water based on the difference of movement alone. There does not seem to be any reason to think that the composition of the water was different as the pond leaked badly and was completely renewed within 48 hr. Nor does it appear to be simply the strength of the current as one has never observed such fundamental differences in the

Table 8. *Nos./sq.mm. of certain dominant algae growing on glass slides in the river Itchen, February–June* 1935

No. of days submerged ...	Cocconeis				Achnanthes spp.				Gomphonema spp.			
	5	10	20	30	5	10	20	30	5	10	20	30
Date submerged												
25. vi. 35	785	—	—	—	341	—	—	—	68	...	—	—
15. vi. 35	158	180	—	—	351	640	—	—	11	48	—	—
4. vi. 35	107	129	68	—	89	200	0	—	9	6	9	—
25. v. 35	118	3756	2144	1985	341	1088	347	1909	29	6	12	45
14. v. 35	118	111	2138	2691	41	79	112	27	36	4	0	3
4. v. 35	159	630	500	1688	67	304	773	115	9	134	4	0
24. iv. 35	118	189	1238	—	64	220	724	—	18	32	207	—
12. iv. 35	28	1349	1307	2874	1	536	58	1271	3	44	0	215
2. iv. 35	127	671	2636	—	58	146	262	—	32	66	27	—
23. iii. 35	16	207	1223	3667	14	182	502	816	2	19	30	27
13. iii. 35	65	404	2753	—	25	339	631	—	7	307	44	—
3. iii. 35	13	40	1544	1642	1	21	1387	896	4	7	956	40
21. ii. 35	—	104	931	401	—	27	1913	3231	—	7	7	3432
11. ii. 35	—	—	72	2096	—	—	57	318	—	—	11	20
1. ii. 35	—	—	—	428	—	—	—	789	—	—	—	1204

No. of days submerged ...	Nitzschia palea				Ulvella				Chamaesiphon sp.			
	5	10	20	30	5	10	20	30	5	10	20	30
Date submerged												
25. vi. 35	112	—	—	—	182	—	—	—	220		—	—
15. vi. 35	62	120	—	—	11	47	—	—	48	16		
4. vi. 35	118	265	3	—	24	18	0	—	0	18	5570	—
25. v. 35	268	67	6	0	14	191	24	394	14	1529	5944	973
14. v. 35	155	41	0	0	2	497	59	2	18	0	5782	5274
4. v. 35	84	254	684	32	29	152	13	124	0	145	117	5447
24. iv. 35	29	209	211	—	0	54	418	—	10	4	1044	—
12. iv. 35	1	80	4	26	0	113	413	488	1	164	4640	3474
2. iv. 35	12	0	0	—	0	11	664	—	37	120	1665	—
23. iii. 35	1	11	21	0	1	31	354	358	2	38	770	2186
13. iii. 35	3	25	62	—	0	48	387	—	4	127	1489	—
3. iii. 35	1	2	62	0	0	1	142	449	0	4	413	3675
21. ii. 35	—	0	0	0	—	12	489	548	—	1	1006	187
11. ii. 35	—	—	4	0	—	—	9	4	—	—	3	61
1. ii. 35	—	—	—	312	—	—	—	187	—	—	—	40

For the progressive change in a given set of slides read horizontally.
For the seasonal variation with a constant period of submergence read vertically upwards.
For the quantities on a given set of slides collected the same day read diagonally.

slowest and fastest portions of the river as, for example, above and below the Alresford weir. Nor is there apparently any difference in temperature, light or oxygen content. There is clearly some physical difference in still and running water connected simply with movement. The algae obtain substances for their metabolism entirely from the water surrounding them. In a river this watery medium is being continually renewed over the algal surface, while in a pond this movement is very slow and irregular, and consequently impoverishment of the dissolved food substances can take place in the film adjacent to the algae. The statement very frequently made that running or turbulent water means good aeration is of course incorrect, as a pond full of green plants contains during the day far more oxygen than any rapidly flowing river. What does happen in rapidly moving water is that that there is a rapid and continuous renewal of raw material over the surface of any submerged solid.

If this conception be correct several important conclusions follow. The increasing rapidity of growth with increasing current is to be expected up to a point when the algal

growth cannot make use of all the food substances presented to it in the passing water. Beyond this point growth will probably be stationary and removal of organisms will be more and more rapid. The greatest change in the composition of a water or watery solution of salts will take place when it is flowing as a shallow stream rapidly over a film of growing organisms. Repurification of polluted waters will thus be most rapid in small shallow streams where there is an abundant growth on the bed, though our knowledge of the metabolism of both algae and phanerogams is not sufficient to say what part they take in the breakdown of organic matter as distinct from the action of the bacteria and fungi with which they are naturally associated.

Another consideration is that for estimates of dissolved salts and other food substances in relation to algal growth, comparative concentrations from running water and still water are meaningless. Considerably smaller concentrations are clearly sufficient to maintain growth if the solution over an algal colony is being continuously renewed than where the film is almost stationary and liable to be depleted. Strict comparison also cannot be made between slow and fast rivers unless quantities are expressed in relation to the discharge of the water past a given point.

ENCRUSTATION

Many writers (e.g. Tilden, 1897; Fritsch, 1943) have noted and commented upon the precipitation of calcium carbonate and the formation of a chalk encrustation among certain fresh-water algae. This precipitation is very obvious among the algal growths on the glass slides used in this investigation. There does not appear to be in the literature any clear-cut explanation of this phenomenon.

The chemical reaction $CaCO_3 + H_2O + CO_2 = Ca(HCO_3)_2$ is a reversible one and the bicarbonate is an unstable salt. In water the free CO_2 is removed by the assimilating green plants and since the equilibrium is disturbed, more CO_2 is released from the bicarbonate, and calcium carbonate, being insoluble, *must* be precipitated. This precipitation takes place, therefore, whenever green plants are assimilating in calcareous waters and the precipitate usually comes down in the form of calcite crystals. It is not confined to any particular species of alga nor even to the algae as a group, and it can equally well take place on the submerged leaves of flowering plants. There is, however, to be explained the extreme cases of incrustation around *Gongrosira*, *Chaetophora* or *Rivularia*. This can be accounted for by the ability of a body mechanically to hold and consolidate the crystals after they are formed. A completely flat parenchymatous disk will have no retaining power; a mucilaginous mass will retain quite a lot, and clearly a mass of small anastomising filaments, as developed almost to perfection in *Gongrosira*, will entangle and grow over and consolidate considerable quantities. The absence or presence of a chalk crust is of no taxonomic value whatever, and forms distinguished on the basis of this character, e.g. *Chaetophora calcarea* Tilden (1897), should be considered to have no status except to indicate that the plant grows in hard water. The *Ulvella-Cocconeis* community will develop equally well in hard or soft water, and calcite crystals are always present in the former case. Chalk crusts were also observed on the grains of sand in filter beds at the Metropolitan Water Board (1939), and it is quite easy to see how the sand which is filtering out bacteria and assimilating algae will also retain and consolidate the calcite crystals liberated by the latter.

SUMMARY

Quantitative estimations of the algal growths on the river bed of the Itchen, Test and Hampshire Avon have been made for more than a year at frequent intervals.

The total quantities fluctuate considerably but show generally a single annual cycle with maximum in midsummer and minimum in winter.

The average quantity increases downstream in response, it is suggested, to the progressive eutrophication of the water.

The average nos./sq.mm. of glass-slide surface lie between 2000 and 10,000, a quantity found in all eutrophic waters.

Quantities are larger where the current is fast than where it is slow.

There is a single algal community throughout the year dominated by *Cocconeis*, *Ulvella* and *Chamaesiphon*. There are a few other algae that vary markedly in quantity, e.g. *Gomphonema*, but their maxima have not been at the same time each year. Apart from these there appears to be no seasonal variation.

The above community increases with the progressive eutrophication of any river and is considered to represent the climax association of algae in any river.

Marked differences in the community were observed in a pond fed by and adjacent to the river, and these differences are assigned to the physical fact of movement of the water over the algal film.

An explanation of the calcium crust is suggested.

REFERENCES

Butcher, R. W. (1927). *J. Ecol.* **15**, 55.

Butcher, R. W. (1940). *J. Ecol.* **28**, 210.

Butcher, R. W. (1938). *Avon Biol. Res. Rep. Southampton*, **5**, 47.

Butcher, R. W., Longwell, J. & Pentelow, F. T. K. (1931). *Rep. Wat. Pollut. Bd, Lond.*, no. 6.

Butcher, R. W., Pentelow, F. T. K. & Woodley, J. W. A. (1937). *Fish Invest.* Series 1, **3**, no. 3.

Fritsch, F. E. (1943). *Structure and Reproduction of the Algae.* Cambridge.

Godward, M. (1934). *Beih. Bot. Zbl.*

Metropolitan Water Board (1939). *33rd Ann. Rep.* London.

Pearsall, W. H. (1923). *J. Ecol.* **11**.

Pentelow, F. T. K., Butcher, R. W. & Grindley, J. (1938). *Fish. Invest.* Series 1, **4**, no. 1.

Rice, C. H. (1938). *Ann. Bot., Lond.*, N.S. **2**.

Tilden, J. E. (1897). *Bot. Gaz.* **23**.

APPENDIX

List of algae found in the Itchen (I), Test (T), and Hampshire Avon (A) during the experiments, 1933–38

		I.	T.	A.
CHLOROPHYCEAE				
Chlamydomonas daceae		r.	—	—
Gonium pectorale Mull.	In pond	r.	—	—
Pandorina morum (Mull.) Bory	In pond	r.	—	—
Sporotetras pyriformis Butcher	Woodmill	f., r.	c.	c.
Characium sieboldi A. Br.		v.r.	—	r.
C. strictum A. Br.	In pond	c.	—	v.r.
? *Chlorella pyrenoidosa* Chick		s.d.	m.	m.
Sphaerobotrys fluviatilis Butcher	In pond	d., f.	s.d.	s.d.
Pediastrum boryanum (Turp.) Men.		—	—	r.
Scenendesmus bijugatus (Turp.) Kutz.		r.	v.r.	r.
S. obliquus (Turp.) Kutz.		—	v.r.	—
S. quadricauda (Turp.) Breb.		r.	—	—

Ulothrix aequalis Kutz.	At times	s.d.	f.	**r.**
U. zonata (Web. & Mohr.) Kutz.		f.	r.	f.
Cladophora glonerata (L) Kutz.		m.	m.	m.
Stigeoclonium falklandicum Kutz.		f.	m.	c.
S. farctum Berth. var. *anglicum* Butcher		d.	s.d.	c.
S. tenue Kutz.		m.	m.	c.
Chaetophora elegans (Roth) Ag.		r.	—	—
?Protoderma sp.	At times	s.d.	m.	f.
Ulvella frequens Butcher		d.	d.	d.
Gongrosira sclerococcus Kutz.		c.	—	c.
G. schmidlei P. Richter		r.	c.	—
Coleochaete scutata Breb.	In pond	c.	—	—
Chaetopeltis orbicularis Berth.	In pond	s.d., r.	r.	—
?Chaetopeltis sp. as in Hull	In pond	c, —	m.	—
Oedogonium spp. indet.		r.	r.	r.
Vaucheria sp. indet.		m.	m.	r.
BACILLARIOPHYCEAE-DIATOMS				
Melosira varians Ag.		**r.**	m.	**r.**
M. distans (Ehr.) Kutz.		r.	—	—
Cyclotella meneghiniana Kutz.		r.	r.	r.
C. comta (Ehr.) Kutz.		—	—	r.
Diatoma vulgare Bory		f.	f.	f.
Meridion circulare Ag.		f.	r.	—
Fragilaria intermedia Grun.		m.	**r.**	**m.**
F. leptostauron (Ehr.) Hust.		c.	r.	m.
F. capucina Desmaz.		r.	r.	—
Synedra ulna (Nitzsch.) Ehr.		f.	f.	f.
S. acus Kutz.		r.	r.	—
Cocconeis placentula Ehr.		d.	d.	d.
C. pediculus Ehr.		m.	r.	—
Achnanthes microcephala Kutz.		r.	—	—
A. minutissima Kutz.		d.	d.	d.
A. linearis W. Sm.		f.	m.	r.
A. lanceolata Breb.		s.d.	s.d.	s.d.
Rhoicosphenia curvata (Kutz.) Grun.		r.	r.	r.
Frustulia rhomboides (Ehr.) de Toni		r.	—	—
Gyrosigma Acuminatum (Kutz.) Rab.		r.	r.	m.
Navicula cryptocephala Kutz.		m.	m.	m.
N. viridula Kutz.		r.	m.	m.
N. cari Ehr.		—	—	r.
N. reinhartii Gr.		c.	r.	—
N. menisculus Schum.		—	—	m.
N. gracilis Ehr.		c.	c.	m.
Pinnularia viridis (Nitzsch) Ehr.		r.	—	—
Amphora ovalis Kutz.		f.	f.	s.d.
Cymbella aspera (Ehr.) Cleve		r.	—	r.
C. parva (W. Sm.) Cleve		m.	—	—
C. affinis Kutz.		—	—	r.
C. ventricosa Kutz.		s.d.	s.d.	s.d.
Gomphonema acuminatum Ehr.		r.	r.	—
G. parvulum (Kutz.) Grun.		m.	m.	c.
G. angustatum (Kutz.) Rab.		—	—	r.
G. constrictum Ehr.		m.	m.	m.
G. olivaceum Lyngb.		d.	d.	d.
Denticula tenuis Kutz.		r.	—	—
Nitzschia dissipata (Kutz.) Grun.		f.	f.	m.
N. amphibia Grun.		—	r.	r.
N. palea (Kutz.) W. Sm.		d.	d.	d.
N. acuta Hantzsch.		r.	m.	r.
N. acicularis W. Sm.		m.	m.	—
Cymatopleura solea (Breb.) W. Sm.		r.	r.	r.
Surirella ovalis Kutz.		—	—	m.
CHRYSOPHYCEA				
Heterolagynion oedogonii		r.	r.	m.
MYXOPHYCEAE				
Chamaesiphon incrustans Grun.		d.	d.	d.
C. regularis (Fritsch) Geit.		d.	d.	d.
Phormidium foveolarum (Mont.) Gom.		s.d.	s.d.	s.d.
P. retzii (Ag.) Gom.		m.	r.	—
Oscillatoria limosa Ag.		r.	—	—

REVIEWS

Harvey, H. W. *Recent Advances in the Chemistry and Biology of Sea water.* Pp. 164, 29 figures. 10s. 6d. Cambridge University Press.

The unusual features of the marine habitat and the difficulties arising during the study of marine-habitat conditions, come partly from the fact that the metabolism of marine organisms often differs from that of terrestrial creatures and partly from the fact that marine habitats are almost always in a state of rapid change. Technically speaking then, sequences of observations in one place deal neither with the same water nor with the same organisms, and, in order to obtain a reasonable picture of ecological events in the sea, observations must be taken over a far larger space and on a far larger scale than is necessary in other habitat types. It has thus often appeared that the vast amount of marine research carried out within the last thirty years had yielded an ecological harvest which was considered to be disappointingly small, when compared with the wide scale of the investigations. The present book will show that, in fact, a position has now been reached when integration is possible and that the harvest is impressive and will undoubtedly continue to be so.

In the investigation of the marine habitat in strongly tidal conditions, the Plymouth laboratory has taken a leading part and it has, in particular, been to the especial credit of some of the Plymouth workers that they early appreciated the fact that real advance was only possible if some, at least, of the biological problems involved could be isolated, as it were, under cultural conditions in the laboratory. The particular problems which have come to be associated with this field of work are hence those which are especially suitable in their final stages for cultural and laboratory analysis — those concerned with the utilization of mineral materials by marine plants and with their subsequent role in the production of animals. In short, those problems cover what might well be called the metabolic ecology of the marine plankton.

This book deals, first, with the data necessary to the analysis of the problems and, secondly, with the evaluation and integration of the facts obtained. The points of view are not separated, though it is obvious that integration becomes more possible in the later stages of the book and hence more prominent towards the end. The subjects treated include, first, a survey of the physical characters of the water masses, including those based on salinity or chlorinity, and then follows, secondly, a wide survey of the chemical characteristics, which includes both major and minor constituents and the dissolved gases. There follow next chapters on the biologically important constituents containing nitrogen and phosphorus, the methods employed in their estimation, the regeneration of nutrient salts and the changes caused by bacterial action. Lastly comes a discussion on the role of these and other factors in the growth of phyto-plankton and their bearing on the magnitude of the standing crop of plants and animals in the marine plankton.

It may be said of this book that it is marked by the accurate presentation of fact and by the careful evaluation of its relevance. It gives a coherent picture of the present state of the subjects with which it deals, a picture which gains enormously in depth and colour from the author's intimate acquaintance both with the problems investigated and with the future explorations which will be necessary. It is an important book to any biologist and one which is indispensable to those interested in aquatic biology.

W. H. P.

Howard, Sir A. *Farming and Gardening for Health or Disease.* Pp. 282, plates 15 and figures 5. 12s. 6d. London: Faber and Faber.

No doubt most ecologists, who are interested in soil conditions, would agree that the essential features of natural soil fertility are associated with the soil humus and with the micro-organisms that live on it. Sir Albert Howard's views on this subject are well known, and the present book emphasizes them once again. It focuses attention on the value of composts as an essential feature in the recuperation of a cropped soil, with new illustrative material drawn both from England and South Africa.

The book as a whole is concerned more largely with the thesis that the health of plants, and of animals feeding on these plants, is dependent upon soil fertility and, by inference, upon soil fertility as induced by humus composts. The view is one which is becoming increasingly fashionable and, attractive as it may be, it will not be verified easily, nor, it may be suggested, by the methods employed in this book. The treatment of the subject adopted includes an interesting survey of ancient agricultural methods and

useful references to the yields obtained from them. There is, further, a survey of different crop plants and their diseases, largely as they are believed to be affected by compost treatments. The wide range of information is both interesting and useful, but, readable as the various sections are, the treatment is too wide always to carry conviction. It is, moreover, difficult to believe that scientific agriculturalists are at once so biased and so incompetent as they are represented to be, even though many botanists will sympathize with the author's revolt against the purely laboratory attitude in soil investigations.

The book has two considerable virtues. In the first place, its readability will help it to keep before the public certain fundamental principles of soil maintenance and crop production. In the second place, it serves a valuable purpose in stating the argument that disease is commonly associated with some form of unsuitable nutrition. Hence it will generally be easier to prevent disease (by removing possible causes) than to try and find, or to use, remedial treatments when the malady appears.

W. H. P.

Tansley, A. G. *Our Heritage of Wild Nature.* Pp. 74, 26 photographs. Cambridge University Press.

This book is a reasoned demand for the preservation of the wild life in the British Isles. It deals rather fully with the nature of the problem, with descriptions of the communities, both animal and vegetational, which are left for preservation, and with the measures which are advocated to effect that preservation. Nature Reserves, the work of the Forestry Commission and of the National Trust, the need for education of the general public and the role of National Parks are all treated at length, and the final conclusions emphasize the need for knowledge and for a National Wild Life Service. While it is inevitable that there is a certain similarity of viewpoint between this book and the recent reports published by the British Ecological Society, the present volume gains enormously not only from its more elegant style but also from the magnificent photographs with which it is illustrated. It is a work one can freely recommend.

W. H. P.

CHANGES IN VEGETATION DUE TO THE WAR

J. D. Grose. The Impact of War on the Wiltshire Flora. *Wiltsh. Archaeol. Nat. Hist. Mag.* **1**, 336–345, 1944.

This short paper by an experienced field botanist who is an acute observer contains a wealth of interesting and instructive records.

The war-time activities most damaging to our native flora were found to be the wholesale felling of woods —a loss which will be permanent and disastrous if they are replanted with alien conifers—and the clearance and ploughing of scrub and heathland which have destroyed, probably permanently, some rare Wiltshire species. The ploughing of lowland pastures and of great areas on the gentler slopes of the downs will not, Mr Grose believes, have a permanent effect, because he thinks that such areas will be allowed to revert to their former condition. But if the Government's intention to maintain the great wartime extension of our agricultural area is carried into effect most of this newly ploughed land will remain arable, and this is not a result of the war with which we can rightly quarrel.

Weeds of cultivation, such as *Lychnis githago, Centaurea cyanus* and *Melampyrum arvense*, have reappeared in newly cultivated ground and many other species, both weeds and members of established semi-natural communities, have migrated extensively, appearing in tank tracks and on slopes bared and scored by the traffic of heavy vehicles. Railway tracks, no longer sprayed with weed-killer, have been abundantly colonized by many species, and a new branch railway which has been very little used has produced an extraordinary mixture of members of cornfield, heath, pasture and woodland communities with weeds of waste ground. Water plants, presumably brought by visiting birds, have very rapidly vegetated Home Guard trenches which had become filled with water, and the range of many has thus been greatly increased. A quarter-mile stretch of an overgrown canal was cleared of vegetation and converted into a Fire Service water supply, and comparative lists from the overgrown canal, the same a year after clearing, and the spoil from the canal bed at two different dates in 1942, show a remarkably large collection of species (117 in all) and illustrate a number of ecological processes. Roadside verges have been neglected, and several species have increased upon them; while on one neglected lawn the bee and fly orchids have appeared. The author expects that the flora will largely return to its previous condition when peace returns, except for the native woodland trees and some heathland rarities.

A. G. T.

PAPERS OF ECOLOGICAL INTEREST RECEIVED

Albertson, F. W. & Weaver, J. E. Effects of drought, dust, and intensity of grazing on cover and yield of short-grass pastures. *Ecol. Monogr.* **14**, 1944.

Beard, J. S. Climax vegetation of tropical America. *Ecology,* **25**, 2, 1944.

Beard, J. S. The natural vegetation of the island of Tobago, British West Indies. *Ecol. Monogr.* **14**, 1944.

Carlisle, D. B. & Cuany, R. L. Brereton Pool. *N.W. Nat. Union Yearb.* 1941–3.

Chapman, V. J. Methods of surveying *Laminaria* beds. *J. Mar. Biol. Ass. U.K.* **26**, 1944.

Chapman, V. J. Cambridge Univ. Exped. to Jamaica. Pt. 1. A study of the botanical processes concerned in the development of the Jamaican shore-line. Pt. 2. A study of the environment of *Avicennia nitida* Jacq. in Jamaica. Pt. 3. The morphology of *Avicennia nitida* Jacq. and the function of its pneumatophores. (*Bot.*), *J. Linn. Soc.* **52**, no. 346, 1944.

Clausen, J., Keck, D. D. & Hiesey, W. M. Experimental studies on the nature of species. II. Plant evolution through amphiploidy and autoploidy, with examples from the Madinae. *Publ. Carneg. Instn,* no. 564, 1945.

Davies, R. D. & Milton, W. E. J. Direct reseeding on upland peat. *Welsh J. Agric.* **18**, 43, 1945.

Eardley, Constance M. An ecological study of the vegetation of Eight Mile Creek Swamp, a natural South Australian coastal fen formation. *Trans. Roy. Soc. S. Aust.* **67**, no. 2, 1943.

Fagan, T. W., Jones, E. & Williams, E. E. The influence of liming on the herbage of acidic soils in Merioneth-shire. *Welsh J. Agric.* **18**, 73, 1945.

Fritsch, F. E. Marine biological research in Great Britain. *Nature, Lond.,* **154**, 1944.

Jones, G. N. *Flora of Illinois.* University Press Notre Dame, Ill.

Knoche, Walter. Algunas observaciones microclimaticas en La Mina Aguilar-Bolivia. *An. Soc. cient. argent.* **4**, 137, 1944.

Richards, P. W. The biogeographic division of the Indo-Australian Archipelago. 6. The ecological segregation of the Indo-Malayan and Australian elements in the vegetation of Borneo. *Proc. Linn. Soc. Lond.* **154**, pt. 2, 1943.

Richards, P. W. The floristic composition of primary tropical rain forest. *Biol. Rev.* **20**, 1945.

Richards, P. W. The taxonomy of British bryophytes as a field for research. *Nature, Lond.,* **155**, 1945.

Scourfield, D. J. The nannoplankton of bomb-crater pools in Epping Forest. *Essex Nat.* **27**, pt. 9, 1944.

Stephenson, T. A. Causes of intertidal zonation. *Nature, Lond.,* **150**, 1942.

Stephenson, T. A. Causes of the vertical and horizontal distribution of organisms between tidemarks in South Africa. *Proc. Linn. Soc. Lond.* **154**, pt. 3, 1943.

Stephenson, T. A. The constitution of the intertidal fauna and flora of South Africa. II. *Ann. Natal Mus.* **10**, pt. 3, 1944.

Weaver, J. E. Replacement of true prairie by mixed prairie in eastern Nebraska and Kansas. *Ecology,* **24**, no. 4, 1943.

Weaver, J. E. Recovery of Midwestern prairies from drought. *Proc. Amer. Phil. Soc.* **88**, no. 2, 1944.

Weaver, J. E. & Darland, R. W. Grassland patterns in 1940. *Ecology,* **25**, no. 2, 1944.

Welch, Paul S. The hatchet planimeter as a limnological instrument. *Linn. Soc. Amer. Spec. Publ.* no. 14, 1944.

Welten, Max. Pollenanalytische, stratigraphische und geochronologische Untersuchungen aus dem Faulen-seemoos bei Spiez. *Veröff. geobot. Inst. Rübel,* **21**, 1944.

Williams, W. Varieties and strains of red and white clover—British and foreign. *Bull. Welsh Plant Breed. Sta.* H 16, 1945.

BRITISH ECOLOGICAL SOCIETY

ANNUAL MEETING IN THE BOTANY SCHOOL, CAMBRIDGE

9–10 JANUARY 1945

Tuesday, 9 January

The winter meeting of the Society was opened in the afternoon of Tuesday, 9 January, in the Botany School, Cambridge, with the assembling of a large number of members and guests at an exhibition of ecological material arranged in the big elementary laboratory. Dr H. Hamshaw Thomas had set out an exhibit of photographs and herbarium specimens illustrating ferns from the high mountain vegetation of Jamaica, at altitudes between 5000 and 7500 ft., rainfall over 100 in., and constant high humidity. Among the genera represented were *Cyathea*, *Gleichenia*, *Hymenophyllum*, *Elaphoglossum*, *Rhipidopsis*, *Diplazium* and *Lophosoria*, often with fronds of immense size. Mr T. G. Tutin showed seedlings of *Juniperus communis* from seeds collected on the Fleam Dyke near Cambridge, now germinating very sparsely. Dr M. H. Clifford had set out a series of photographs illustrating vegetation and scenery of the Cambridge district, the Fenland, and the Norfolk coast. Dr P. W. Richards exhibited a cultivated specimen of *Bartramia pomiformis* and herbarium specimens showing to what a great extent direct variation of environmental conditions affects the morphology of certain plastic moss species such as *Hypnum cupressiforme* and *Sphagnum subsecundum*, whilst the non-plastic species such as *Breutelia chrysocoma* are little affected. Distinct forms from different habitats but of unknown (possibly genetic) status were exhibited of other mosses such as *Tortula ruraliformis* and *Porotrichum alopecurum*. Genetic races of *Dactylis glomerata* were set out by Mr J. Crespin to demonstrate a series from lax types of low tillering capacity to those which are dense and tiller freely. Of the two, the former are short-lived under grazing, but naturally favoured in seed production. Dr V. J. Chapman exhibited maps, herbarium specimens, and photographs illustrative of his paper to be given at the meeting upon British saltmarsh species of *Suaeda* and *Obione*. Mr J. Rishbeth produced a striking exhibit of the flora of Cambridge walls and buildings. The lists, which included 128 species of flowering plants, were compared with those of Cambridgeshire pollard willows, and of the church roofs of Poitiers. He conclusively illustrated by living samples a succession of stages, first from colonization by mosses, through invasion by flowering plants, and finally to a lichen degeneration of the moss-mat, possibly through the effects of bird droppings. Dr A. S. Watt had put out a book of the annotated photographs of the Cambridge Botany School ecological expedition to the Cairngorms in 1938–9. Mr H. W. Howard set out an exhibit showing by dried specimens and photographs the appearance of the diploid watercress, *Nasturtium officinale*, the artificially made autotetraploid derived from it, and the naturally occurring allopolyploid, to which it is proposed the name *N. uniseriatum* should be given, and the sterile triploid hybrid between the last and *N. officinale*. Distribution maps for the wild forms were shown for Europe, Britain and Cambridgeshire. The newly recognized species has seeds arranged in a single row on the replum (as in *Cardamine*), a lower stomatal index than *N. officinale*, and seeds with more numerous and smaller alveoli, as well as a more straggling habit in culture.

Some 70 or 80 members and guests were present at a soirée held the same evening in the Combination Room of Clare College. At the close of a most enjoyable social gathering Dr O. W. Richards expressed the thanks of the Society to the Master and Fellows for the use of the Combination Room. The meeting dispersed about 11 p.m.

Wednesday, 10 January

At 10 a.m. on Wednesday, 10 January, the Annual General Meeting opened with the reading and signing of the minutes of last year's annual meeting, and with the reading of apologies for absence from Dr Turrill Prof. Buxton, Mr Elton, Dr Watson, Dr Chitty, Dr Southern and Prof. McLean.

The following were elected to membership of the Society: Mr J. Spedan Lewis, Mr G. Waterson, The Isle of Wight Natural History and Archaeological Society, Mr R. G. West, Mr C. A. Connell, Mr J. Rishbeth and Dr D. A. Webb. Mr Venables' resignation was reported.

The report of the Hon. Secretaries upon the work of the Society in 1944 was read and accepted in the form already approved by the Council.

Report of the Secretaries for the year 1944

The thirtieth Annual Meeting of the Society was held in the University Department of Botany, Oxford, on 5 and 6 January 1944. On 5 January the meeting began with a pleasant social evening at which films and lantern slides were shown, and where members were able to examine a large range of ecological material set out in the laboratories. The business meeting was opened next day at 10 a.m., and after the business had been concluded a series of six most interesting ecological addresses was given to the Society. We are very happy to thank Prof. Osborn and his colleagues for their hospitality and their energetic assistance with the meeting, and Mrs Osborn and her assistants for the provision of refreshment on a bountiful scale.

The Council has again found it impracticable to hold a summer meeting of the Society, but a well-attended one-day meeting was held on Tuesday, 21 March, in London, where a lively and informative discussion was held on 'The Ecology of Closely Related Species'. We are grateful to the Linnean Society of London for permission to use their rooms for this meeting, and for the convenience they have given us throughout the war in allowing us the use of a room for Council meetings.

During the year printing difficulties have again very much retarded publication of our journals, but the second number of the 1944 volume of each journal is due to appear directly. In both journals space has been devoted to the publication in full of the Council's report on 'Nature Conservation and Nature Reserves'. The 1944 volume of the *Journal of Ecology* contains also a full report of the joint meeting with foresters, under the title 'Ecological Principles involved in the Practice of Forestry',* together with seven original articles, as well as reviews and accounts of the Biological Flora. The two parts will contain respectively 142 and 112 pages.

Volume 13 of the *Journal of Animal Ecology* will be of about 185 pages, containing eleven original articles, as well as notices, reviews, and an extensive series of notices of publications on the animal ecology of the British Isles. Publication of the Biological Flora continues very satisfactorily with the appearance of accounts of *Tamus communis*, and of the genus *Acer* with three of its species. The editors devote much time and energy to this project and have an impressive list of accounts in preparation.

The Society's report on Nature Conservation has been very kindly received by the press and interested administrative bodies, and it will interest members to learn that the Cambridge University Press has published a small illustrated book by Prof. Tansley, called *Our Heritage of Wild Nature*, in which the author expresses at a popular level the basic ideas on which the Nature Conservation report itself was framed. Negotiations continue between the Council and other interested bodies with a view to securing action along the lines indicated in the Nature Conservation report, and partly with this in mind the Council has applied for the Society to be admitted to membership of the Parliamentary and Scientific Committee.

During the year we have to record with regret the death of Prof. J. H. Priestley, who in times past has been host to the Society at Leeds, and of our French colleague, M. Pierre Allorge. The membership of the Society has risen since last year from 398 to 420 members, 7 members having resigned or died, and 29 new members having been elected. Of the present membership 225 receive the *Journal of Ecology* alone, 132 the *Journal of Animal Ecology* alone, 61 take both journals, and 2 neither.

H. GODWIN
L. A. HARVEY } *Hon. Secretaries*

The Hon. Treasurers gave a provisional report of the financial position of the Society, suggesting that with the grant of £150 from the Royal Society, and the excellent progress of collection of subscriptions and repayment of arrears, the Society might expect a surplus of perhaps £250 to £300 on the year's working. The thanks of the Society to the treasurers for their devoted and successful work were

* See also reports of the meeting in *Forestry* and in *Nature*.

moved from the chair and carried unanimously. On the proposal of the President it was agreed that Messrs Wm. Norman and Sons be reappointed auditors to the Society, and on the proposal of Prof. Pearsall it was agreed that a grant of £10 be made to the Freshwater Biological Association for 1945.

The meeting then proceeded to the election of Officers as follows:

> *Hon. Secretaries:* H. GODWIN, L. A. HARVEY.
> *Hon. Editors:* W. H. PEARSALL, C. ELTON.
> *Hon. Treasurers:* V. S. SUMMERHAYES, A. S. WATT.
> *Ordinary Council Members:* T. G. B. OSBORN, C. B. WILLIAMS.

Prof. Pearsall reported that there was a present abundance of good papers for the *Journal of Ecology*, and coupled a request for brevity with a hope that there should be a continued flow of contributions. He apologized for unavoidable delays in printing. Prof. Clapham reported that a total of nineteen accounts had now appeared in the Biological Flora, that others were ready for press, and many were in preparation.

Prof. Tansley reported that a small committee of the Council had been drawing up a memorandum upon the importance of ecological science in relation to Nature Conservation, with recommendations as to the creation of a Central Authority under whose auspices these matters might be considered at the national level. It was proposed to publish this memorandum and send it to the administrative bodies concerned. Major Hume said that the Universities' Federation for Animal Welfare had been promoting a Wild Life Service intended to co-ordinate the interests concerned. Dr Chapman asked that Mr Steers, adviser to the Ministry of Town and Country Planning, be kept informed of these activities.

Dr H. H. Thomas spoke strongly of the importance of air survey to ecological research, and of the importance that material already secured should become available to scientists. He suggested that a photographic reconnaissance unit of the R.A.F. should be kept in being after the war, and become the core of a service available for many national purposes, including scientific research. Dr V. J. Chapman and Capt. C. Diver supported these views, and the following resolution was carried unanimously by the meeting: 'That this meeting considers it most desirable that the Aerial Photographic Survey material secured by the Royal Air Force should be made available for scientific purposes, that a photographic reconnaissance unit of the R.A.F. should be actively maintained after the war, that its services be made widely available for scientific purposes: and requests the Council of the Society to take suitable action on this matter.'

The President, Dr O. W. Richards, then delivered his extremely stimulating presidential address upon 'Ecology from the View-point of the Entomologist'.

After the lunch adjournment Dr V. J. Chapman read his paper on 'British Species of *Suaeda* and *Obione*'. His outline of the autecology of these species included discussion of the various ecological features of the varieties *vulgaris, macrocarpa* and *flexilis* of *Suaeda maritima*, and of ecovars *latifolia* and *parvifolia* of *Obione portulacoides*. Comparison was made between British and American distribution data, and reference was made to culture experiments in soil of varying salinity. In the discussion afterwards Mr Howard, Dr O. W. Richards, Dr Godwin, Prof. Tansley and Prof. Pearsall took part.

Mr C. H. Gimingham then gave an account of 'The Structure of Bryophytic Communities on Rocks in the Lake District'. He demonstrated that such communities possess a basic structure which remains more or less constant in regard to life-form, but that from habitat to habitat the same life-form will be represented by different bryophytic species. He contrasted the short compact turf or dwarf cushions of thallose and compact leafy liverworts typical of open communities with the plagiotropic mat-forming aggregates of creeping forms in the closed communities, and compared the proportions of species of a given life-form class to be found in each of the six habitats comprised by the boulders in (1) mountain streams, (2) lake sides, (3) woods, (4) walls, (5) siliceous mountains and (6) limestone mountains. He illustrated a succession from an open associule through to a closed mat stage as a climax, with possibly a post-climax in places of rapid soil accumulation. An active discussion followed, in which the following took part: Dr V. J. Chapman, Dr E. W. Jones, Mr T. A. Oxley, Major C. W. Hume and Mr L. A. Harvey.

There then followed an account by Mrs Dainton of 'The Activity of Slugs'. This was an account of the investigation of those sensory responses of the grey field slug, *Agriolimax reticulatus*, which led to its phases of activity. Experiment contradicted the suggestion that humidity affects activity, and light proved stimulatory but transient. The slugs proved, however, to be very sensitive to small decreases of temperature, responding to as little as one-tenth of a degree Centigrade per hour. This response was

correlated convincingly with slug activity in natural conditions, the fall of temperature very commonly accompanying rainfall adequately explaining slug activity with the onset of rain. In the subsequent discussion Dr H. F. Barnes, Dr V. J. Chapman and Mrs L. A. Harvey took part.

Dr A. S. Watt gave the concluding paper of the meeting on the topic 'Bracken versus Heather'. The chief ecological characteristics of the two species were contrasted, the one geophytic, frost-sensitive, tall, a woodland inhabitant, and intolerant of deficient soil aeration; the other phanerophytic, frost-hardy, light-demanding, and associated with acidic and raw-humus soils. It was concluded that over a certain range of habitats *Pteridium* may permanently suppress *Calluna* without anthropogenous disturbance; in other habitats grazing causes suppression of *Calluna*, and in yet others *Calluna* may suppress *Pteridium*. Prof. Pearsall, Prof. Tansley and Dr le Cren took part in the discussion following the paper.

The meeting was concluded with the expression by the President of the Society's most cordial thanks to Prof. Brooks for the use of his department, and to Mrs Godwin, Mrs Watt and their many colleagues for their provision of generous refreshment.

BIOLOGICAL FLORA OF THE BRITISH ISLES

ACCOUNTS PUBLISHED OR IN PREPARATION

The parts already published are:

Juncus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.

J. inflexus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.

J. effusus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.

J. conglomeratus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.

J. subnodulosus Schrank, by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.

*Zostera L., *Z. marina* L. and *Z. hornemanniana* Tutin, by T. G. Tutin. *J. Ecol.* **30**, no. 1.

Cladium mariscus R.Br., by V. M. Conway. *J. Ecol.* **30**, no. 1.

Aster tripolium L., by A. R. Clapham, W. H. Pearsall and P. W. Richards. *J. Ecol.* **30**, no. 2.

Juncus filiformis L., by P. W. Richards. *J. Ecol.* **31**, no. 1.

J. macer Gray, by P. W. Richards. *J. Ecol.* **31**, no. 1.

*Rhamnus cathartica L. and *Frangula alnus* Mill, by H. Godwin. *J. Ecol.* **31**, no. 1.

Tamus communis L., by I. H. Burkill. *J. Ecol.* **32**, no. 1.

Acer campestre L. and *A. pseudo-platanus* L., with a note on *A. platanoides* L., by E. W. Jones. *J. Ecol.* **32**, no. 2.

*Polygonum L. em Gaertn., *P. persicaria* L., *P. lapathifolium* L. and *P. petecticale* (Stokes) Druce, by N. W. Simmonds. *J. Ecol.* **33**, no. 1.

Gentiana pneumonanthe L., by N. W. Simmonds. *J. Ecol.* **33**, no. 2.

These may be obtained from the Cambridge University Press, 200 Euston Road, N.W. 1, at 1*s.* each; those marked with an asterisk are sold as double parts, 2*s.* Standing orders for all parts issued may be placed at the reduced price of 9*d.* each, double parts 1*s.* 6*d.*

The following are being prepared:

Aconitum anglicum Stapf, H. A. Hyde, National Museum of Wales, Cardiff.

Adoxa moschatellina L., Prof. M. Skene, The University, Bristol.

Allium ursinum L., T. G. Tutin, University College, Leicester.

A. vineale L., Mrs R. H. Richens, c/o The Botany School, Cambridge.

Andromeda polifolia L., Prof. W. H. Pearsall, F.R.S., Department of Botany, University College, Gower St, W.C. 1.

Anemone nemorosa L., A. C. Crundwell, Loadhams, Farnham, Surrey.

Arenaria verna L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

A. norvegica Gunn., Dr W. A. Clark, King's College, Newcastle-on-Tyne.

Arum maculatum L., F. A. Sowter, 9 North Avenue, Leicester.

Asperula odorata L., Prof. A. R. Clapham, Department of Botany, The University, Sheffield.

Atropa belladonna L., Dr R. W. Butcher and Dr W. O. James, University Dept. of Botany, Oxford.

Blackstonia perfoliata (L.) Huds., Dr B. Colson, University Department of Botany, Reading.

Carlina vulgaris L., *Cirsium palustre* (L.) Scop. and *C. vulgare* (Savi) Airy-Shaw (*C. lanceolatum* (L.) Scop.), Dr W. A. Sledge, University Department of Botany, Leeds 2.

Colchicum autumnale L., Dr R. W. Butcher, Culford House, Ewe Lamb Lane, Bramcote, Notts.

Corallorrhiza trifida Châtel., Prof. J. R. Matthews and Dr Downie, University Department of Botany, Old Aberdeen.

Cuscuta europaea L., Bernard Verdcourt, 86 Claremont Rd, Luton, Beds.

Danaa cornubiensis (L.) Burnat, Dr G. Pethybridge, Penlee, Harleigh Rd, Bodmin.

Daphne laureola L., Dr P. W. Richards, The Botany School, Cambridge.

Elymus arenarius L., T. E. T. Bond, Tea Research Institute, Ceylon.

Epilobium nummularifolium R.Cunn., Miss A. J. Davey, Dept. of Botany, Memorial Buildings, Bangor.

Eriocaulon septangulare With., Dr Leighton Hare, Jodrell Laboratory, Royal Botanic Gardens, Kew.

Galium erectum Huds. and *G. mollugo* L., Miss M. Priestley, c/o The Botany School, Cambridge.

Glaux maritima L., Miss C. M. Gibson, Municipal College, Portsmouth.

Glyceria maxima (Hartm.) Holmb., Miss J. M. Lambert, Westfield College, Oxford.

Goodyera repens R.Br., Prof. J. R. Matthews and Dr Downie, University Department of Botany, Old Aberdeen.

Helictotrichon (*Avena*) *pratense* (L.) Pilger and *H. pubescens* (Huds.) Pilger, Dr G. Carson, School of Agriculture, Cambridge.

Juncus articulatus L., em. Wahlenb. and *J. acutiflorus* Ehrh. ex Hoffm., Prof. A. R. Clapham, Department of Botany, The University, Sheffield.

J. squarrosus L., Prof. W. H. Pearsall, F.R.S., University College, Gower St, London, W.C. 1.

J. triglumis L., Dr W. A. Clark, King's College, Newcastle-on-Tyne.

Juniperus communis L., T. G. Tutin, University College, Leicester.

Leontodon leysseri (Wallr.) Beck (*Thrincia hirta* Roth) and *L. hispidus* L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Leucojum aestivum L., Dr F. B. Hora, University Department of Botany, Reading.

Limosella aquatica L., Dr F. W. Jane and Miss R. Dowling, Department of Botany, University College, Gower St, London, W.C. 1.

L. subulata Ives, Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Listera cordata (L.) R.Br., Prof. J. R. Matthews, University Department of Botany, Old Aberdeen.

Lloydia serotina (L.) Reichb. and *Lobelia dortmanna* L., Dr N. Woodhead, University Department of Botany, Bangor, North Wales.

Luzula forsteri (Sm.) DC. and *L. pilosa* (L.) Willd., Prof. T. Harris, University Department of Botany, Reading.

Melandrium dioicum (L.) Coss. & Germ. and *M. album* (Mill.) Garcke, H. G. Baker, University Department of Botany, Leeds 2.

Myosotis arvensis (L.) Hill, *M. collina* Hoffm. and *M. versicolor* Sm., A. E. Wade, National Museum of Wales, Cardiff.

Myrica gale L., Miss A. J. Davey, Dept. of Botany, Memorial Buildings, Bangor.

Naias flexilis Rostkov, Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.

Narcissus pseudo-narcissus L., Dr J. Caldwell, University College, Exeter.

Nardus stricta L., R. Elfyn Hughes, Department of Agricultural Botany, Bangor.

Narthecium ossifragum (L.) Huds., Dr Mollison, University Department of Botany, Old Aberdeen.

Nasturtium officinale R.Br., H. W. Howard, School of Agriculture, Cambridge.

Obione portulacoides (L.) Moq., and *O. pedunculata* (L.) Moq., Prof. V. J. Chapman, c/o Botany School, Cambridge.

Ophrys arachnites Hoffm., Francis Rose, The Forge House, East Malling, Kent.

Orchis fuchsii Druce, *O. elodes* Gris., *O. latifolia* L. sec. Pugsl. (*O. incarnata* auct. angl.) and *O. purpurella* Stephenson, Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.

O. purpurea Huds., Francis Rose, The Forge House, East Malling, Kent.

Oxalis acetosella L., Miss Ethel Bolton, King's College, Newcastle-on-Tyne.

Potamogeton coloratus Hornem., *P. filiformis* Pers. and *P. pectinatus* L., Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.

P. gramineus L. and *P. rutilus* Wolfg., Dr W. A. Clark, King's College, Newcastle-on-Tyne.

Quercus robur L. and *Q. petraea* (Mattuschka) Liebl., Dr E. W. Jones, Imperial Institute of Forestry, Oxford.

Ranunculus aquatilis agg., Dr R. W. Butcher, Culford House, Ewe Lamb Lane, Bramcote, Notts.

Rhynchospora alba (L.) Vahl and *R. fusca* (L.) Ait. f., Miss E. Canton, Department of Biology, Technical College, Sunderland.

Rosa spp. (excl. *R. arvensis*, *micrantha* and *tomentosa*), Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.

Rumex spp., J. E. Lousley, 7 Penistone Road, Streatham Common, S.W. 16.

Scilla non-scripta (L.) Hoffmanns. & Link, Dr G. E. Blackman, Imperial College of Science, London, S.W. 7.

Sedum acre L., Dr B. Barnes, Department of Biology, Chelsea Polytechnic, London, S.W. 3.

Sinapis arvensis L., G. E. Fogg, Department of Botany, University College, Gower St, W.C. 1.

Sonchus asper (L.) Hill and *S. oleraceus* L., emend. Hill, R. A. Lewin, c/o The Botany School, Cambridge.

S. palustris L., Francis Rose, The Forge House, East Malling, Kent.

Spiranthes stricta Nels., Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.

Stellaria nemorum L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Subularia aquatica L., Dr N. Woodhead, Department of Botany, Bangor.

Suaeda fruticosa (L.) Forsk., and *S. maritima* (L.) Dum., Prof. V. J. Chapman, c/o Botany School, Cambridge.

Thlaspi alpestre L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Tilia cordata Mill. and *T. platyphyllos* Scop., H. A. Hyde, National Museum of Wales, Cardiff.

Trientalis europaeus L., Prof. J. R. Matthews, University Department of Botany, Old Aberdeen.

Ulmus spp., Dr R. Melville, The Herbarium, Royal Botanic Gardens, Kew.

Urtica spp., P. Greig-Smith, Department of Botany, The University, Manchester.

Vaccinium vitis-idaea L., P. A. Tallentire, 14 Hulme Hall Avenue, Cheadle Hulme, Cheshire.

Valeriana officinalis L. and *V. sambucifolia* Mikan, J. Carpenter, Department of Botany, King's College, Strand, W.C. 2.

Viburnum lantana L. and *V. opulus* L., Dr H. Godwin, The Botany School, Cambridge.

Viola lutea Huds. and *V. tricolor* L., Dr P. E. Fothergill, King's College, Newcastle-on-Tyne.

Wahlenbergia hederacea Reichb., Francis Rose, The Forge House, East Malling, Kent.

The assistance of members of the Society will be greatly welcomed by the authors who are preparing these accounts. Information should be sent direct to the addresses given above. Anyone wishing to write an account singly or in collaboration should communicate with one of the members of the Committee or with the Hon. Secretary of the Society.

Accounts ready for publication should be sent to Dr P. W. Richards, Botany School, Cambridge.

BIOLOGICAL FLORA OF THE BRITISH ISLES

L.C. (Ed. 11) No. **1377**

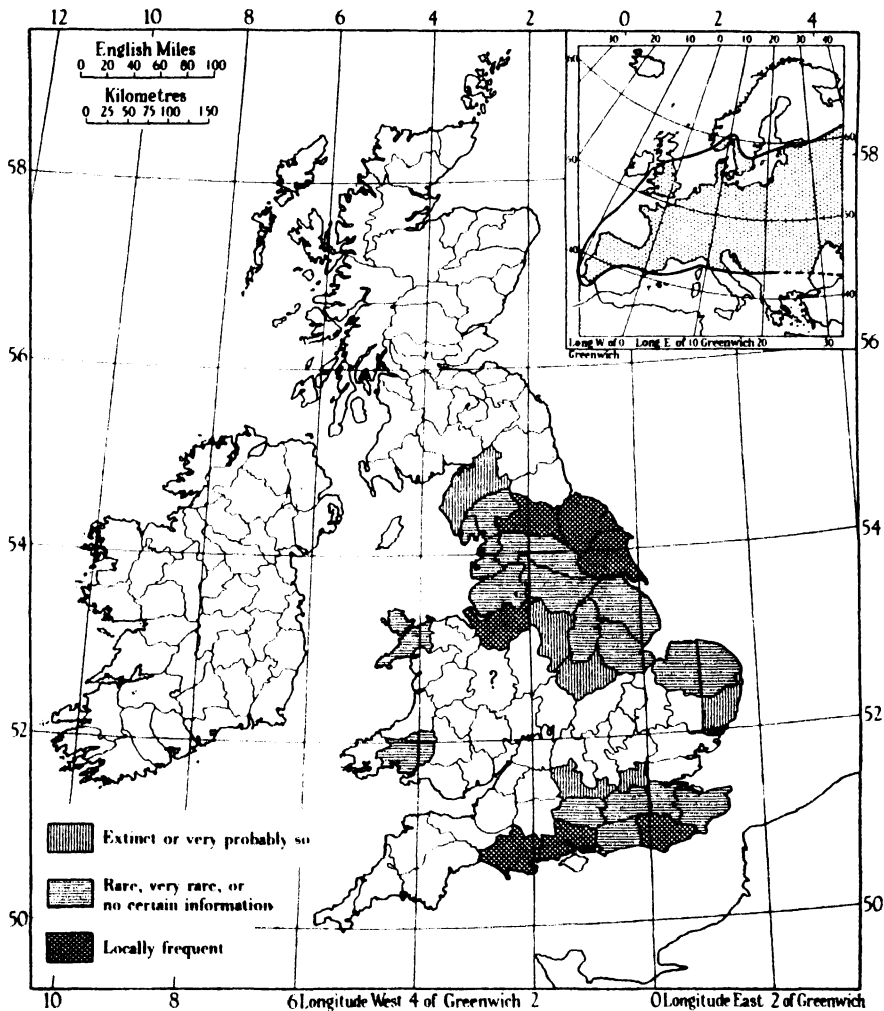## Gentiana pneumonanthe L.

N. W. SIMMONDS*

Fig. 1. *Gentiana pneumonanthe* L. Vice-comital distribution in the British Isles and (inset) distribution in Europe.

Sect. PNEUMONANTHE. An erect glabrous perennial, with flowering stems up to about 18 in. (45 cm.) high, usually unbranched. Lower leaves small bracket-like, upper linear or occasionally lanceolate, with reflexed margins. Flowers all terminal, or terminal and axillary, subsessile; calyx with 5 linear-lanceolate teeth; corolla 1–2 in. (25–50 cm.)

* The MS. was left incomplete by Mr Simmonds on his departure for Trinidad. The Editors considered it desirable to publish it in its present state.

long, deep blue with longitudinal greenish stripes, plicate, lobes 5, acute, green-spotted within. Stamens 5, the anthers coherent. Ovary on gynophore, stigmas reflexed. Seeds minute, winged.

Varies in size, habit, number of shoots, shape of leaves, number and colour of flowers. Thus Robinson (1913) observed variation in size and width of leaves on East Winch Common, Norfolk; he noted that plants with more than one flower were rare and found a white-flowered variety. (i) Size: between $2\frac{3}{4}$ and 18 in. (7–45 cm.) high in east Dorset, 1943; 12–40 cm. high (average about 28 cm.) in east Norfolk (E. A. Ellis). (ii) Number of shoots: usually 1 flowering shoot, frequently with 1 or 2 small vegetative shoots; 2 or more flowering shoots are occasionally found. Vegetative shoots may bear undeveloped flower buds (east Dorset, 1943). (iii) Habit: normally erect and unbranched, but stems more or less branched or decumbent at the base occur (see below and III). (iv) Leaf shape: normally linear, but may be lanceolate or ovate-lanceolate (see below). (v) Number of flowers, see VIII (*g*); from 1 to 14 flowers per stem in east Dorset, 1943, and 1–28 (commonly 5–15) in east Norfolk (E. A. Ellis), but Hegi (*Fl.* **5**, p. 2001) mentions a plant with 82 flowers. (vi) Flower colour: the shade of blue varies somewhat, usually it is deep. White flowers have been seen on St Leonard's Common, Dorset (1943), and are recorded from west Norfolk (Robinson, 1913), Surrey (Salmon, 1931, p. 455) and the Continent (Hegi, *Fl.* **5**, p. 2001); f. *albiflora* Murr. is perhaps the same as the horticultural 'variety alba'. F. *roseiflora* Zinserling has rose-pink flowers such as those recorded by Johnson (1927) in Anglesey and by E. A. Ellis in Norfolk; the var. *carnea* (no authority given) mentioned by Rayner (1929, p. 70) from Hampshire is probably the same. The status of all these varieties is unknown.

Continental writers appear to agree in accepting three varieties, none of which has hitherto been recorded as British; these are var. *latifolia* Lec. & Lam., var. *minor* (*depressa* Boiss., *humilior* Car. & St. Lag.) and var. *diffusa* Griseb. The last-named has the stems decumbent at the base, many flowered and the foliage leaves broadly ovate-lanceolate; plants corresponding more or less with this description have been found on St Leonard's Common, Dorset (certain identification is not at present possible; specimen in Herb. Mus. Brit.). There is some evidence that all these 'varieties' are mere forms (see IV, below).

A lowland species, in the British Isles practically confined to a characteristic type of damp, acid heathland in England and Wales; rare, but locally fairly common.

I. *Geographical and altitudinal distribution.* Found in two main blocks of vice-counties, in England and Wales. (i) The southern block consists of: 9 (Dorset), 11 and 12 (Hants), 13 and 14 (Sussex), 15 and 16 (Kent) and 17 (Surrey). Extinct in 21 (Middlesex) and 22 (Berks). Recorded by Druce (*Comit. Fl.*, p. 201) for 8 (Wilts S.), but there is no confirmation of this. The record for 24 (Bucks) in *Top. Bot. Suppl.* 2 is not confirmed by Druce in his county flora (1926, p. 229). (ii) The northern block consists of: 27 and 28 (Norfolk), 44 (Carmarthen), 49 (Caernarvon), 52 (Anglesey), 53 and 54 (Lincs), 56 (Notts) 58 (Cheshire), 59 and 60 (Lancs), 61–65 (Yorks), and 69 (Westmorland). Extinct in 25 (east Suffolk), 55 (Leicester and Rutland), 57 (Derby) and 70 (Cumberland). In addition there is a specimen in the Cambridge University Herbarium (label not in the collector's handwriting) from 'Llanymynach, Shropshire' dated 1829; *G. pneumonanthe* is not recorded in the 'Flora of Shropshire' (Leighton, 1841) and no other record for the county is known.

The species is thus present in 25 and extinct in 6 vice-counties. The markedly discontinuous distribution is probably due in part to a lack of suitable habitats in central England. This region, broadly, is characterized by basic soils and intensive agriculture, neither of which is favourable to the plant. Out of the six vice-counties in which it has become extinct, four lie on the margin of the present area of distribution and adjacent to the region of central England under consideration. The failure of the species to occur farther north and west is perhaps due to climatic limitation and the more mountainous nature of the ground. It is a lowland species with, on the whole, a rather 'Continental' distribution (though it reaches south-west Portugal); lack of suitable habitats may also be involved.

Rare, but locally frequent. Said to be decreasing in many localities and will probably be lost to several more vice-counties, if this has not already occurred (see IV).

Throughout central Europe, northern Spain, Portugal, northern Italy and the Balkans, excluding Greece; south-east Norway, southern Sweden, Estonia, Karelia and east to the Urals, Siberia and Kamchatka, central and southern Russia to the Caucasus, the mountains of central Asia and the Baikal region (details of distribution in central Asia not known). To 59° 15′ N. in Norway (Blytt, 1906, p. 577) and to about 61° N. by Lake Ladoga (Hermann, 1912, p. 373). Southern and western European limit in Portugal at about 9° W. and 38° N.

A lowland species; to 800 ft. (246 m.) in Westmorland (Wilson, 1938, p. 185) and rarely above 3900 ft. (1200 m.) in central Europe (Hegi, *Fl.* 5, p. 2001). Distribution in the Swiss Alps subalpine-montane, according to Schroeter (*Pflanzenleben*, p. 539), to 1770 ft. (540 m.) in Graubünden (Braun-Blanquet & Rübel, 1933, p. 1108).

Restricted to rather open habitats, though the young shoots may have to grow up through shade. In cultivation sunshine is desirable (T. C. Mansfield).

II. *Habitat.* (1) Almost limited in Britain to one type of damp acid heathland. In east Dorset, generally occurs in the transition from heath with a podsol profile to topogenous *Sphagnum* bog with a peat soil. The characteristic profile consists of a layer of well-humified surface peat overlying sand or sandy peat of variable colour: a pan or 'B' horizon is not present but there is evidence of the occurrence of some leaching. Probably controlled by the presence of a relatively high ground-water table, dependent on local topography. In east Norfolk, where *G. pneumonanthe* is locally common on a few peaty heaths, it occurs in two localities approximately on the 100 ft. (33 m.) contour at the extreme source of streams rising in shallow depressions (E. A. Ellis).

(2) *Substratum.* (a) *Parent material.* Forty-eight localities in the Dorset heathlands studied by R. D'O. Good were exclusively on Tertiary deposits. In east Dorset, the parent material is generally Bagshot Sands which are mainly sandy beds with some clay and pebbles. It has also been seen on Valley Gravel at St Leonard's Common, Dorset. In Norfolk it occurs on Glacial Drift (E. A. Ellis, C. P. Petch).

(b) *Soil profile.* Typically consists of up to 9 in. (23 cm.) of dark, well-humified peat, rather 'greasy' to the touch, overlying sand or sandy clay of variable colour: this peat appears to correspond with 'greasy duff', 'greasy mor' or 'amorphous peat' mentioned by Clarke (1941, pp. 74 et seq.). The underlying sand may be grey, white or reddish yellow and is commonly more or less coarsely mottled: in some cases (see Fig. 2, no. 3), the top few inches are markedly paler in colour than those below; this probably represents the initial stages of podsolization, since nearby sections show an unmistakable though slight

development of a 'B' horizon. This is in accord with the pH changes found in the profile (see (g), below). Robinson (1932, p. 238) states however that there may be some bleaching of the surface layers of the mineral soil as a result of the reduction of ferric to ferrous iron consequent upon the occurrence of a high and fluctuating water-table. The characteristic coarse mottling noted above probably corresponds with the gley. In Norfolk it is found on peat over typical podsol profiles (E. A. Ellis).

Depth cm. in.	1	2	3	4	5
0 — 0	Black peat (pH 4·4)	Black peat and peaty sand passing into	Black peat	Raw, unhumified Sphagnum peat	Pale, fibrous peat
10 —			Peaty sand		Greyish brown sand
5	Peaty sand (pH 4·72) passing to		Greyish white sand		
20 —	Whitish and yellow, mottled clayey sand with some flint pebbles (pH 5·03)		Reddish grey mottled clayey sand with clay more abundant locally	Black, greasy peat	
10		Greyish and yellow mottled sand with clay and pebbles		Reddish sand with clay and gravel	
30 —					
15					Whitish sand
40 —					
50 — 20					
60 —					
25					
70 —					
30					

Fig. 2. Five soil profiles from the Dorset heathlands to illustrate the soil types on which *Gentiana pneumonanthe* grows. Nos. 1 and 3 are from a heath between West Moors and Ferndown and nos. 2, 4 and 5 from St Leonard's Common. (All pH figures electrometic.) For discussion, see text.

Occurs also in a topogenous *Sphagnum* bog on Creech Heath, Dorset; the profile given in Fig. 2, no. 4 clearly represents an approach to such conditions. These two cases, together with another profile on St Leonard's Common in which the pale fibrous peat at the surface appears to have originated from old *Molinia* shoot-bases (Fig. 2, no. 5), are, however, somewhat exceptional. Another exceptional soil has been noted at Clapham, Yorks, by Dr W. A. Sledge who regards thin peat overlying sand as typical, much as in Dorset; this

is a 'stiff, impermeable glacial clay' where the species is accompanied by some equally unusual associates (see III, below).

To take a general view of the soil profile, the absence of the characteristic podsol 'B' horizon, very well developed on similar substrata nearby in the Dorset heathlands, is probably due to soil-water conditions, in particular, the ground-water table. *G. pneumonanthe* grows in hollows where a complete gradation may often be observed between Callunetum and topogenous *Sphagnum* bog. Although no details about the water-table are available, it is noteworthy that, at least in some stations, our species is liable to winter flooding, if only temporarily, e.g. on a heath between West Moors and Ferndown, Dorset. The soil is therefore probably a ground-water type controlled by a high water-table and owing its existence to local topography. Robinson (1932, p. 238) notes the occurrence of local space series from podsol through meadow-soil to peat, developed in hollows in podsol regions. Such series are marked by an increase in thickness in the surface humus, the disappearance of the characteristic podsol horizons and the development of a gley layer. It is in the middle of such series that the species grows in Dorset and Norfolk (see (1) above).

More tolerant on the continent than in Britain. Thus Rübel (1930, p. 275) notes that it occurs in neutral or slightly basic Molinieta in north-east Switzerland, while Braun-Blanquet & Rübel (1933, 2, p. 1108) state that it is characteristic of Molinieta on clayey lime-rich soils on the Rhine alluvia of Graubünden. But for the most part it seems to occur on acid, often peaty soils.

With regard to requirements under cultivation, T. C. Mansfield says: 'It should be cultivated on sandy, peaty soils where the lime content is as low as possible.'

(*g*) *p*H. All measurements are acid. See Fig. 2, no. 1, determined electrometrically by H. Paver who also determined two surface peat samples from St Leonard's Common as 4·20 and 4·54. Many other Dorset readings by the capillator method all gave acid values. It will be seen from Fig. 2, no. 1, that there occurs a decrease in *p*H towards the surface; this is to be expected if there has been some leaching of the surface layers (see (*b*)). In two Norfolk localities the *p*H (colorimetric) at 0–12 cm. varied from 5·0 to 6·0 (J. Lambert).

(*h*)–(*k*) The results of Pearsall's modified ammonium thiocyanate test (with and without addition of hydrogen peroxide) on samples from two east Norfolk localities indicated that the soils were oxidizing; the diphenylamine test agreed with this, showing that all the samples were nitrifying (J. Lambert).

(3) (*a*) *Light intensity.* In Dorset often in rather open habitats, but young shoots may have to grow up through bushes of *Erica tetralix*. Restricted to open habitats in Norfolk (E. A. Ellis).

(*b*) *Humidity.* Often grows in hollows in which mist and fog collect and which may contain permanently saturated soil, so at least tolerates high humidity.

(*c*) *Exposure to wind.* No information about tolerance.

III. *Communities.* Rather constantly associated with *Erica tetralix* and the non-tussocky form of *Molinia caerulea*. Typically found in a community consisting of bushes of *Erica* with *Molinia* scattered over the intervening more or less bare peat surface. Most commonly found between the bushes, but sometimes occurs under them, the stems either growing right through or coming out laterally from a decumbent base. Some kind of cyclical relationship between the *Erica* and the *Molinia* has been suggested, but this has not been investigated. Fig. 3 is a typical metre quadrat on a heath between West

Moors and Ferndown, Dorset (June 1944). It appears that plants of *Gentiana pneu-monanthe* become included in confluent tussocks of *Erica*, though the majority of them lie on the intervening peat.

Calluna vulgaris (as low sparse shoots, not as bushes), *Sphagnum* spp. (in small dense tufts), *Drosera* spp. (also on bare peat), *Narthecium ossifragum*, *Carex panicea*, *Eleocharis multicaulis* and *Scirpus caespitosus* (the last two not distinguished in the field) are all characteristic associates in Dorset.

A number of lists of associates from Dorset and Norfolk are given in Table 1. Localities 1, 4, 5, 6 and 7 are all fairly typical for Dorset. No. 3 is interesting in containing *Salix*
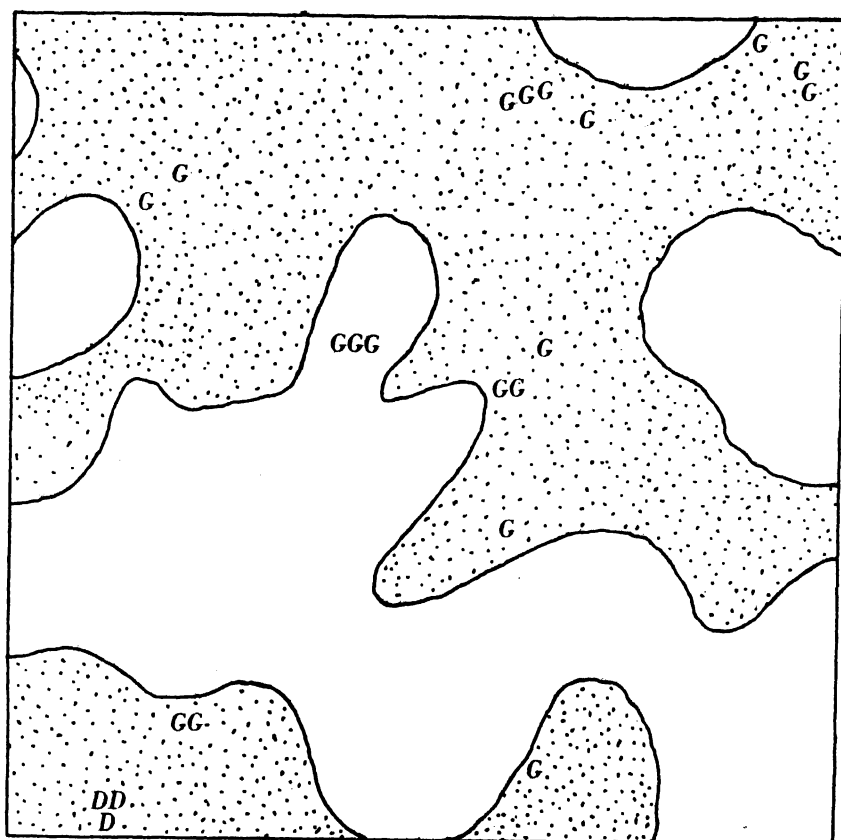

Fig. 3. Quadrat (1 sq.m.) to show the distribution of stems of *Gentiana pneumonanthe* (G) and *Drosera rotundi-folia* (D) in a typical community consisting of tussocks of *Erica tetralix* with *Molinia caerulea* (plain) on an exposed peat surface with scattered shoots of *Molinia* and *Erica* (stippled). (Heath between West Moors and Ferndown, Dorset, 20 June 1944.)

repens and *Ulex minor*, both normally found in drier habitats than those in which *Gentiana pneumonanthe* occurs; there are no soil data for this locality. In nos. 8 and 9 the very local *Erica ciliaris* partly or entirely replaces *E. tetralix*. No. 9 is a list from the bog community alluded to in the section of soils (II (2) above). No. 2 includes some adventive species which arrived after St Leonard's Common had been ploughed up for forestry purposes. List no. 10 is taken from Good (1935, p. 374); the species included are presumably not all immediate associates of *Gentiana pneumonanthe*.

In Lincolnshire *G. pneumonanthe* is found, according to Woodruffe-Peacock (MS. in Botany School, Cambridge), in the '*Erica tetralix* band of saturation'. Robinson (1902,

p. 139) noted that on Skipwith Common, Yorks, 'a profusion of *Gentiana pneumonanthe*' was intermingled with *Calluna*. Dr W. A. Sledge regards moist lowland heath dominated by Ericaceae as the typical habitat in Yorkshire, but states that near Clapham it occurs 'on stiff impermeable glacial clay with grasses, *Nardus*, *Molinia*, and *Deschampsia flexuosa* and *Sphagnum* spp.'

Found in a wider range of communities on the Continent than in Britain. Occurs on *Flachmoore* in Cariceta, Trichophoreta and especially in Molinieta, where it is characteristic but inconstant (Hegi, *Fl.* 5, 2001). In Switzerland found in Molinieta (Schroeter, *Pflanzenleben*, p. 539); characteristic but inconstant in Molinieta in north-east Switzerland (Rübel, 1930, p. 275) and associated there with *Selinum carvifolia*, *Sanguisorba officinalis* and *Serratula tinctoria*. Occurs in meadow land ('*Enzianwiese*') in Prussia (Hegi, *Fl.* 5, 2001) and in the Carpathian foothills, where it is associated with *Rhinanthus* spp. (A. Srodon).

IV. *Response to biotic factors.* Persisted on St Leonard's Common, Dorset, for at least three years after ploughing for forestry purposes: this consists in the cutting of shallow trenches, rectangular in section, about 1 ft. wide, 1 ft. apart and 6 in. deep. The turf removed is thrown to one side and overturned. *Gentiana pneumonanthe* may persist on the strips left undisturbed between the trenches, if not covered by the turf thrown out, and in one case was seen to have grown through the bottom of the overturned sod in which it was growing before being ploughed up. It will presumably be lost to this heath in time.

In one of its east Norfolk localities it has extended its range considerably in the last ten years in spite of frequent heath fires and in another, though subject to horse-grazing and rabbit-nibbling, it does not appear to have suffered (E. A. Ellis).

Drainage, afforestation and picking are probably all important in bringing about the increasing rarity of this species.

Withstands cutting for hay in the meadows of the Carpathians, according to A. Srodon (see III, above).

Rather commonly seen in Dorset on ground which appears to have been disturbed, e.g. in shallow, rectangular depressions of unknown origin. Noticed by H. F. Reynolds on Morden heath, Dorset, on ground which had been disturbed by tank exercises during the 1914–18 war.

Two plants were found in 1943 growing through the spoil from a deep forestry drainage trench dug in 1942, the buds being situated at a depth of 3–4 in. instead of the usual 1 in. or less. One plant had 3 stems with axillary branching, numerous flowers, and very broad leaves: this corresponds with the variety *diffusa* Grisebach. The other had 1 stem with slight axillary branching, 14 flowers and the lower leaves markedly broader than usual. This is at least an approach to the same variety, which may thus be a mere form induced by the deep burial of the buds.

V. (a) *Gregariousness.* Solitary or few plants together or may be locally frequent in a suitable habitat, often of very limited extent. In Norfolk grows singly or in small groups, reaching a density of 30 plants per square metre (E. A. Ellis).

(b) *Performance in various habitats.* No information.

(c) *Effect of frost, drought, etc.* No information.

VI. *Morphology, etc.* See Fig. 4 E. A short vertical or inclined monopodium, up to 1½ in. (3·6 cm.) long, scarred and bearing buds and scale-leaves at the apex. A few thick, whitish, almost unbranched roots are developed adventitiously from the monopodium.

Table 1. Species associated with Gentiana pneumonanthe L. in various localities

Localities

(1) St Leonard's Common, Dorset.
(2) St Leonard's Common, Dorset.
(3) Cranbourne Common, Dorset.
(4) Stoborough Heath, Dorset.
(5) Heath between West Moors and Ferndown, Dorset.
(6) Heath between West Moors and Ferndown, Dorset.
(7) Creech Heath, Dorset.
(8) Creech Heath, Dorset.
(9) Creech Heath, Dorset.
(10) Spur Bog, South Haven Peninsula, Dorset.
(11) West Norfolk locality.
(12) East Norfolk locality A.
(13) East Norfolk locality B. Lower fringe of dry Pteridietum.
(14) East Norfolk locality B. Gentiana belt; Erica tetralix and Molinia co-dominant.
(15) East Norfolk locality B. Zone immediately below (14); Gentiana becoming rare and Erica dominant.
(16) East Norfolk locality B. Cart-track skirting lower edge of (15). Nardus stricta dominant.
(17) East Norfolk locality B. Zone immediately below (16); Genista anglica and Calluna co-dominant.
(18) East Norfolk locality B. Wetter Molinietum immediately below (17); Gentiana scattered over wide area.
(19) East Norfolk locality B. Small wet areas almost completely dominated by Cirsium anglicum (list incomplete).
(20) East Norfolk locality B. Main Gentiana belt near western end, with Erica tetralix and Molinia co-dominant; just below uppermost limit of Erica dominance.

Sources of information: 1–9, N. W. Simmonds; 10, Good (1935, p. 374); 11, C. P. Petch; 12–20, E. A. Ellis.

Column groups: Dorset (1–10); West Norfolk (11); East Norfolk (12–20).

Localities	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Gentiana pneumonanthe	+	+	+	+	+	+	+	+	+	+	a.	c.	f.	c.	o.-r.	f.	o.-r.	o.-r.	l.f.	l.c.
Achillaea ptarmica	—	+	—	—	—	—	—	—	—	—	—	l.f.	—	—	o.-r.	—	o.-r.	o.-r.	—	o.-r.
Agrostis canina	—	—	—	—	—	—	—	—	—	—	—	c.	—	—	—	—	—	—	—	—
A. stolonifera	—	+	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. tenuis	—	—	—	—	—	—	—	—	—	—	—	o.-r.	—	—	—	—	—	—	—	—
Agrostis sp.	—	—	—	—	—	—	—	—	—	—	—	o.-r.	—	—	—	—	—	—	—	—
Anagallis tenella	—	—	—	—	—	—	—	—	—	—	—	l.c.	—	—	—	—	—	—	—	—
Bellis perennis	—	—	—	—	—	—	—	—	—	—	—	f.	—	—	—	—	—	—	—	—
Betula pubescens	—	—	—	—	—	—	—	—	—	—	—	c.	—	—	—	—	f.	—	—	c.
Briza media	—	—	—	—	—	—	—	—	o.	—	a.	c.	—	c.	c.	o.-r.*	c.d.	—	—	o.-r.
Calluna vulgaris	+	+	+	r.-o.	+	+	+	+	o.	+	a.	—	—	—	—	—	—	—	—	o.-r.
Carex echinata	—	—	—	—	—	+	—	—	—	—	r.	—	—	—	—	—	o.-r.	—	—	—
C. flava	—	—	—	—	—	—	—	—	—	—	—	o.-r.	—	—	—	—	o.-r.	—	—	—
C. panicea	—	—	—	l.	+	+	+	+	+	+	—	a.	—	—	—	—	—	—	—	—
C. pulicaris	—	—	—	—	—	+	+	+	+	+	—	—	—	—	—	—	—	—	—	—
Carex sp.	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Centaurea nemoralis	—	—	—	—	—	—	—	—	—	—	—	o.-r.	—	—	—	—	—	l.c.	—	—
Cerastium vulgatum	—	—	—	—	—	—	—	—	—	—	—	o.-r.	—	—	—	—	—	—	—	—
Cirsium anglicum	—	—	—	—	—	—	—	—	a.	—	f.	a.	—	—	—	—	—	f.	c.d.	—
C. palustre	—	—	—	—	—	—	—	—	f.	—	a.f.	o.-r.	—	—	—	o.-r.†	—	—	—	—
Crataegus monogyna	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.-r.†	—	—	—	—
Cynosurus cristatus	—	—	—	—	—	—	—	—	—	—	r.	—	—	—	—	—	—	—	—	—
Drosera anglica	—	—	—	—	+	+	+	+	+	+	o.	o.-r.	—	—	—	—	—	—	—	o.-r.
D. longifolia	f.	—	+	—	—	++	++	++	—	—	—	—	—	l.c.	c.	l.f.	o.-r.	—	—	—
D. rotundifolia	—	—	++	—	—	++	++	++	—	—	—	—	—	—	—	—	o.-r.*	c.	—	o.-r.
Eleocharis multicaulis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Epipactis palustris	—	—	—	—	—	—	—	—	—	—	—	o.-r.	—	—	—	—	a.	f.	—	—
Equisetum palustre	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	c.d.	—
Erica ciliaris	a.	—	—	a.	—	+	+	+	a.	—	d.	—	c.d.	c.d.	—	—	—	—	—	c.d.
E. tetralix	a.	+	+	a.	+	+	+	+	f.	+	r.	d.	c.d.	c.d.	d.	a.	a.	—	—	—
Eriophorum angustifolium	—	—	—	—	—	+	+	+	—	—	—	r.	—	—	—	—	c.	—	—	—
Festuca ovina	—	—	—	—	—	—	—	—	—	—	o.-r.	o.-r.	—	—	—	—	—	—	—	—

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Holcus lanatus	—	—	—	—	—	—	—	a.	—	—	—	—	—	—	—	—	—
H. mollis	—	a.	—	—	o.-r.*	a.	—	a.	—	—	+	—	—	—	—	+	—
Hydrocotyle vulgaris	—	o.-r.	—	—	—	—	l.f.	—	—	—	—	—	—	—	—	—	—
Hypericum elodes	l.f.	—	—	—	—	a.	—	—	—	—	—	—	—	—	—	—	—
H. quadrangulum	—	—	—	—	—	—	—	—	—	—	+	—	—	+	—	+	—
Hypochoeris radicata	l.c.	a.	o.-f.	c.	l.c.	l.c.	l.a.	f.	—	+	—	—	—	—	—	—	—
Juncus acutiflorus	l.c.	—	—	—	—	l.c.	—	—	+	—	—	—	—	—	—	—	—
J. articulatus	c.	f.	a.	—	a.	a.	o.	f.	+	—	—	—	—	—	—	—	—
J. bulbosus	—	—	—	—	—	a.	r.	—	+	—	—	—	—	—	—	—	—
J. conglomeratus (?)	—	—	—	—	—	—	—	f.	—	—	—	—	—	—	—	—	—
J. squarrosus	—	—	—	—	—	—	—	f.	—	—	—	—	—	—	—	—	—
Leontodon leysseri	o.-r.	f.	—	o.-r.	o.-r.	o.-r.	—	o.-r.	+	—	—	—	—	—	—	+	—
Littorella uniflora	f.	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—
Lotus corniculatus	—	—	—	—	—	—	—	f.	—	—	—	—	—	—	—	—	—
L. uliginosus	—	—	—	—	—	—	—	f.	+	—	—	—	—	—	—	+	—
Luzula multiflora	—	—	—	—	—	—	a.	—	+	—	r.	—	—	—	—	—	—
Luzula sp., cf. multiflora	c.d.	—	d.	—	—	—	—	o.-r.	—	—	—	—	—	—	—	—	a.
Lychnis flos-cuculi	—	—	d.	—	—	l.f.	—	l.f.	+	—	—	—	—	—	—	—	—
Lycopodium innundatum	—	—	—	—	—	—	—	d.	+	—	—	—	—	—	—	—	—
Mentha aquatica	c.d.	f.	a.	c.d.	c.	c.d.	a.	d.	+	f.	f.	+	+	+	—	+	f.
Molinia caerulea	—	d.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Myrica gale	—	—	—	—	f.	—	—	—	—	—	—	—	—	—	—	—	—
Nardus stricta	—	f.	—	—	—	o.-r.	—	—	—	—	—	—	—	—	—	—	—
Narthecium ossifragum	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	+	—
Orchis sp., cf. elodes	—	—	—	—	—	—	—	o.-r.	+	—	—	—	—	—	o.	—	—
O. fuchsii	f.	—	—	—	—	—	f.	—	+	—	—	—	—	—	—	—	—
Pedicularis sylvatica	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	+	—
Pinguicula lusitanica	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—
Pinus sylvestris	—	o.-r.†	—	—	—	—	o.-r.†	—	+	—	—	—	—	—	—	+†	—
Plantago lanceolata	—	f.	—	—	—	—	f.	—	+	—	—	—	—	—	—	—	—
Polygala serpyllacea	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—
P. vulgaris	a.	o.-r.	o.-r.	l.f.	o.-r.	o.-r.	o.-r.	—	+	+	—	—	—	—	—	—	—
Potentilla erecta	—	a.	a.	—	l.f.	l.f.	a.	—	+	—	—	—	—	—	—	—	—
Potamogeton polygonifolius	—	c.	—	—	—	—	r.	—	+	—	—	—	—	—	—	+	—
Prunella vulgaris	—	—	—	o.-r.*	—	—	c.	—	—	—	—	—	—	—	—	—	—
Pteridium aquilinum	—	o.-r.	—	—	—	—	o.-r.	—	—	—	—	—	—	—	—	—	—
Pulicaria dysenterica	—	f.†	—	—	—	—	o.-r.†	—	—	—	—	—	—	—	—	—	—
Quercus robur	—	f.	—	—	—	—	f.	—	+	—	—	—	—	—	—	—	—
Ranunculus acris	o.-r.	—	—	—	—	—	l.f.	—	—	—	—	—	—	—	—	—	—
R. flammula	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—
Rhyncospora alba	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—
R. fusca	—	c.	—	—	—	—	l.f.	—	—	—	—	—	—	—	—	—	—
Salix repens	l.f.	—	—	—	—	—	f.	—	+	—	—	—	—	—	—	+	—
Scirpus caespitosus	l.f.	o.-r.	l.f.	c.	—	c.	f.	—	—	—	—	—	—	—	—	—	—
Succisa pratensis	f.	—	—	o.-r.	—	o.-r.	c.	—	+	—	—	—	—	—	—	—	—
Trifolium pratense	—	f.	—	o.-r.	—	o.-r.	o.-r.	—	—	—	—	—	—	—	—	—	—
T. repens	c.	—	—	f.	—	l.f.	l.f.	—	—	—	—	—	—	—	—	+	—
Ulex gallii	—	—	—	—	—	—	f.	—	—	—	—	—	—	—	—	—	—
U. minor	c.	c.	—	—	f.	f.	f.	—	—	—	—	—	—	—	—	—	—
Valeriana dioica	—	—	c.	—	—	—	—	—	—	—	—	—	+	—	—	—	—
Bryophytes:																	
Gymnocolea inflata o.	—	—	—	—	—	—	—	—	—	—	+	—	+	—	—	—	—
Polytrichum juniperinum o.	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—
Sphagnum spp. f.	—	—	c.	—	+	a.	o.	+	a.	+	+	+	+	—	+	—	—

* Marginal. † Seedlings. ‡ May have been confused with *Scirpus caespitosus* in the field.

Four plants in Dorset, 1943, bore 5, 4, 3 and 3 roots respectively but up to 10 have been seen in herbarium material. In one of the Dorset plants the lowermost root was 8 in. (20 cm.) long and grew downwards: the other three were 7, 7 and 6 in. (18, 18 and 15 cm.) and spread laterally at about 1–3 in. (2·5–8 cm.) below the soil surface. This is fairly typical.

In all mature plants seen, one root with a more or less vertical growth was present at the base of the monopodium and probably represented a seedling root. This is commonly seen in herbarium specimens. The roots of young plants (Fig. 4 D) are more branched and probably not all persistent.

(c) *Mycorrhiza.* Stahl (1900, p. 586) found a fungus in the roots of *Gentiana pneumonanthe* growing in the Rhine valley near Strasbourg. An endophytic fungus was present in the roots of a plant from St Leonard's Common, Dorset (1944).

(d) *Perennation.* The aerial stems die right back in the winter and the shoots of the following year spring up from buds situated at the apex of the subterranean monopodium and subtended by scale-leaves. Classed by Raunkiaer (1934, p. 54) as rosette hemicryptophyte since, though not a rosette plant, the foliage leaves are not concerned in perennation. The monopodial axis bears scale-leaves only and he notes it as the only example of this type in the Danish flora. The buds are whitish and up to ½ in. long: 1–3 have been seen on plants in east Dorset, 1943. Their bases lie at 1 in. or less below the soil surface so that there may be an approach towards a geophytic habit in this species. The specimens of 'var. *diffusa*' (IV, above) were truly geophytic.

(e) *Vegetative reproduction.* Not known.

(f) *Longevity.* About 13 scars have been counted on one large monopodium: since two or three shoots may be produced in one year, this probably indicates an age of rather less than thirteen years. Longevity in cultivation about 5 years (T. C. Mansfield).

(g) *Age at first flowering.* Not until the third year at least. In cultivation, flowers in its second year (T. C. Mansfield).

(h) *Frequency of seed production.* Every year, so far as is known.

(i) *Ecotypes.* No information.

(j) *Chromosome number.* $2n = 26$ (Scheerer, 1939).

VII. *Phenology.* (a) Time of maximum root-growth not known.

(b) Shoots first appeared in mid-April 1944, in Dorset.

(c) Time of flowering, August–September. The earliest available record (quoted by Nicholson, 1914, p. 114) is 2 July in Norfolk. Begins to flower in Norfolk in first week of July and reaches its maximum in early to mid-August (E. A. Ellis). Later in the north than in the south (Watson, 1932).

(d) Time of maturation and shedding of seeds. First ripe fruits seen in Dorset on 23 September 1943. Some still remained unshed in July, 1944.

(e) Time and place of germination. Spring and early summer. Seen on bare peat (cf. habitat of mature plant) and on a mat of *Gymnocolea inflata* overlying bare peat.

VIII. (a) *Mode of pollination.* Flowers protandrous, nectar secreted at the base of the ovary. Mature styles reflexed, thus exposing the stigmatic surfaces to insect visitors, typically humble-bees. Cross fertilization thus normally occurs though self-pollination is possible through adherence of pollen to the plicae of the corolla when the flower closes, and subsequent elongation of the corolla so that these plicae are brought into contact with the reflexed stigmas (Knuth, *Poll.* 3, pp. 101–2).

(b) *Insect visitors.* Typically a humble-bee flower. Insect visitors observed in east Norfolk include large numbers of *Meligethes viridescens* F. (Coleoptera), taking both nectar and pollen; a species of thrips was also abundant in the flowers in one locality and a larval neuropteron was seen in a flower in another (E. A. Ellis). *Stenophilia graphodactyla* Treits. has been recorded as locally abundant on the flowers in Dorset (Meyrick, *Lepidopt.* p. 454).

(c) *Cleistogamy.* Graebner (1893, original not seen, quoted by Uphof, 1938) reports a case of cleistogamy in *Gentiana pneumonanthe.*

(d) *Apomixis.* Unrecorded.

(e) *Vivipary.* Unrecorded.

(f) *Hybrids.* No natural hybrids recorded (the only member of the section Pneumonanthe in Britain). A garden hybrid with *Gentiana lagodechiana* (Kusn.) Grossh. ex Möller is recorded by Musgrave (1941), but no details are available.

(g) *Amount of seed.* (i) Per fruit—5 capsules from St Leonard's Common, Dorset, contained respectively 357, 815, 463, 530 and 691 seeds, giving a mean of 571. Salisbury (*Rep. Cap.* p. 116) gives the figures 433, 405, 491, with a mean of 443. One large capsule

Table 2. *Flower production in* Gentiana pneumonanthe *L.: numbers of plants bearing various numbers of flowers (or capsules)*

	No. of flowers or capsules												
	1	2	3	4	5	6	7	8	9	10	11	12	Mean
Cranbourne Common	27	7	9	1	—	—	—	—	—	—	—	—	1·64
Heath between West Moors and Ferndown (1)	68	10	4	—	—	—	—	—	—	—	—	—	1·22
Do. (2)	16	2	0	1	—	—	—	—	—	—	—	—	1·26
Salisbury (1942)	59	37	43	17	14	4	3	0	2	1	0	1	2·68

from a Norfolk locality contained 815 seeds (E. A. Ellis). (ii) Capsules per plant—The data given in Table 2 were obtained from two localities on a heath between West Moors and Ferndown, Dorset, and from Cranbourne Common, Dorset; the data of Salisbury are also given. There are considerable differences between the populations in respect of seed production; thus the Dorset figures give a mean per plant of 770, while those of Salisbury give a mean of 1188 seeds, despite the lower number of seeds per capsule—this is evidently due to the relatively large number of plants with numerous flowers in his material. He says, 'the very striking fluctuations in number of inflorescences of *Gentiana pneumonanthe* in different seasons may represent a fluctuation of population and not merely of flowering specimens'; there is no further information on this point.

(h) *Dispersal.* Presumably wind-dispersed. Four samples of 50 seeds each weighed 2·3, 2·2, 2·2 and 2·1 mg., a mean of 0·044 mg. per seed; Salisbury (*Rep. Cap.* p. 112) gives 0·025 mg.

(i) *Viability.* Out of many hundreds of seeds used in germination experiments, only 8 germinated. Easily grown from seed in gardens (T. C. Mansfield).

(j) *Conditions for germination.* See (i). In the writer's experiments only those seeds which had been subjected to freezing for one week germinated.

(k) *Morphology of seedlings.* See Fig. 4.

IX. *Parasites, diseases.* A specimen in the Babington Herbarium in the Cambridge University Botany School from the Ashdown Forest is infested with *Cuscuta epithymum.* No fungal parasites have been recorded. Seed-eating larvae of a Tortricid moth, *Endo-*
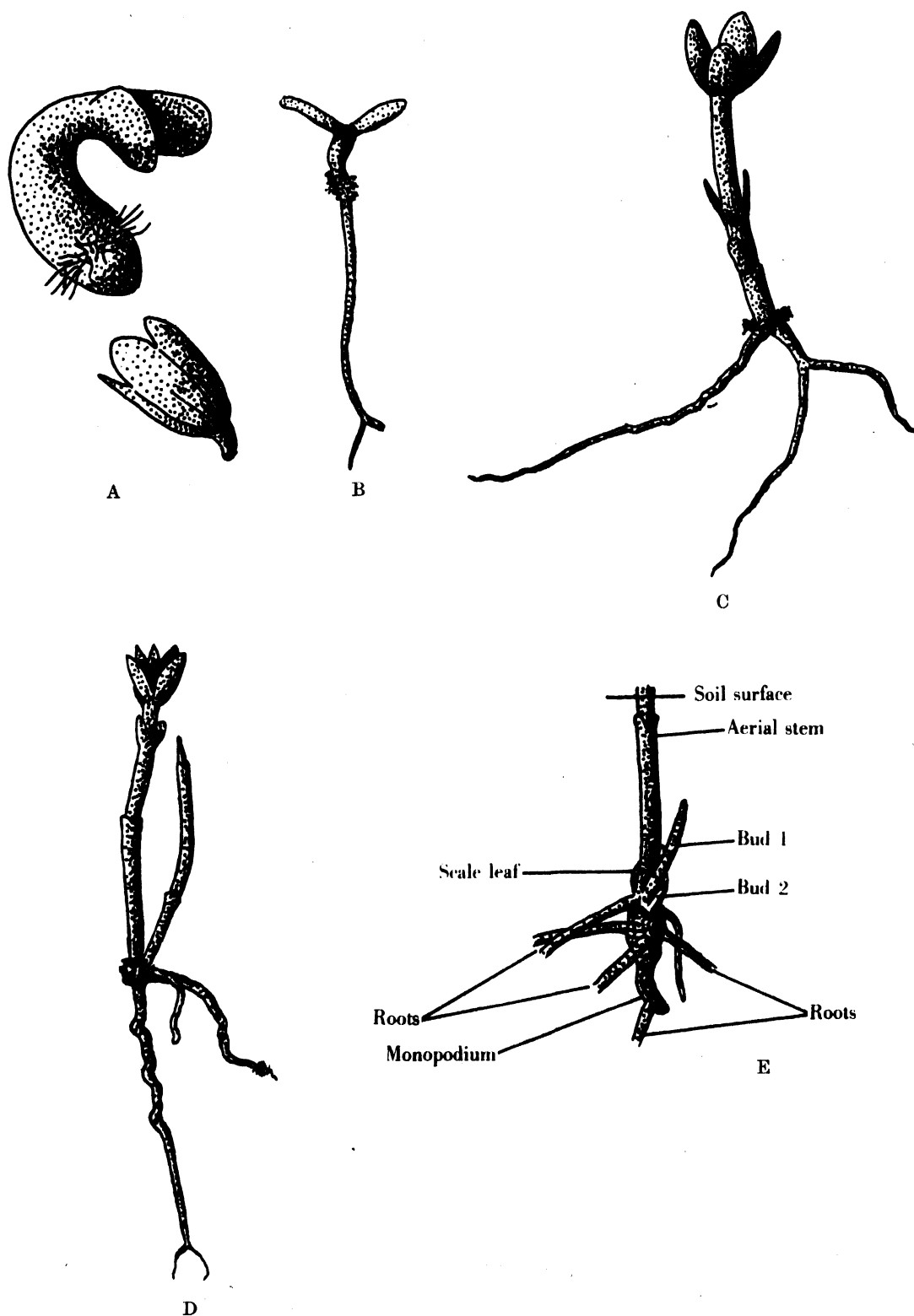
Fig. 4. *Gentiana pneumonanthe* L.   A. Seedlings germinated in the laboratory after about 1 week, × 15. B, C. Older seedlings, B × 10, C × 5.   D. Young plant, Nursery Heath, Dorset, October 1943, × 3. E. Subterranean parts of an old plant, Dorset, September 1943 (nat. size).

thenia gentiana Hb. (*Argyroploce gentianana* Hb.) were frequent in the capsules in a Norfolk locality; these have been recorded from the seedheads of *Dipsacus* and on the Continent from *Gentiana acaulis*, *G. germanica*, *Dipsacus* and *Plantago media* (E. A. Ellis).

X. *History*. A native of Britain, decreasing generally and has become extinct in many localities (see I).

XI. Cultivated for its ornamental flowers.

REFERENCES

Blytt, A. (**1906**). *Haandbog i Norges Flora*. Oslo.

Braun-Blanquet, J. & Rübel, E. (**1933**). *Flora von Graubünden*, 2. Bern und Berlin.

Clarke, G. R. (**1941**). *The Study of the Soil in the Field*. Oxford.

Druce, G. C. (**1926**). *The Flora of Buckinghamshire*. Arbroath.

Good, R. D'O. (**1935**). Contributions towards a survey of the plants and animals of South Haven Peninsula, Dorset. 11. General ecology of flowering plants and ferns. *J. Ecol.* **23**, 361–405.

Graebner, P. (**1893**). Über gelegentliche Kleistogamie. *Verh. Bot. Ver. Brandenburg*, **35**, 148–54.

Hermann, F. (**1912**). *Flora von Deutschland und Fennoskandinavien sowie von Island und Spitzbergen*. Leipzig.

Johnson, A. T. (**1927**). *Rep. B.E.C.* **8**, 311.

Leighton, W. A. (**1841**). *A Flora of Shropshire*. Shrewsbury.

Musgrave, C. T. (**1941**). Features of my garden. V. Gentians at Hascombe. *J. Roy. Hort. Soc.* **66**, 199–206.

Nicholson, W. A. (**1914**). *Flora of Norfolk*. London.

Raunkiaer, C. (**1934**). *Life-forms of Plants and Statistical Plant Geography*. Trans. H. G. Carter. Oxford.

Rayner, J. F. (**1929**). *A Supplement to Frederick Townsend's Flora of Hampshire and the Isle of Wight*. Southampton.

Robinson, F. (**1913**). *Rep. B.E.C.* **3**, 483–4.

Robinson, G. W. (**1932**). *Soils, their Origin, Constitution and Classification*. London.

Robinson, J. F. (**1902**). *Flora of the East Riding of Yorkshire*. London.

Rübel, E. (**1930**). *Das Pflanzengesellschaften der Erde*. Bern.

Salmon, C. E. (**1931**). *Flora of Surrey*. London.

Scheerer, H. (**1939**). Chromosomenzahlen aus der Schleswig-holsteinschen Flora. *Planta*, **29**, 636–42

Stahl, E. (**1900**). Der Sinn der Mycorrhizenbildung. *Jb. wiss. Bot.* **34**, 539–661.

Uphof, J. C. T. (**1938**). Cleistogamic flowers. *Bot. Rev.* **4**, 21–49.

Watson, W. (**1932**). The bryophytes and lichens of moorland. *J. Ecol.* **20**, 284–313.

Wilson, A. (**1938**). *The Flora of Westmorland*. Arbroath.

BRITISH ECOLOGICAL SOCIETY

CHECK LIST OF BRITISH VASCULAR PLANTS

FOREWORD

The purpose of this Check List is not to provide an authoritative statement on the content and taxonomy of the British flora, but to secure uniformity of nomenclature in contributions to the Biological Flora. Contributors will be asked always to use the names appearing in the List unless they can give adequate reasons for doing otherwise. This will obviate the necessity for citing the authorities for names, since it will be understood that the authorities are those cited in the Check List. Thus *Salvia verbenaca* will be understood as referring to *S. verbenaca* L. sec. Pugsl., and not to *S. horminoides* Pourr. (*S. verbenaca* auct., non L.), since only the former application of the name is recommended in the List.

The criterion for inclusion of a name in the List is that it is believed to be the best *binary* name for a taxonomic unit which is at least frequently regarded as having 'specific' rank. It should not be inferred that contributors are bound to recognize all included units as full species. In order to emphasize this point it has been felt useful to set in from the margin names of units whose claim to specific rank is not generally conceded. Contributors may treat such units as subspecies or varieties if they so choose (citing authorities for the names used), but if binary names are used they must be those given in the List. In many instances binary names are also provided for aggregate species (e.g. *Thalictrum minus* agg., *Alchemilla vulgaris* agg.), and contributors are invited to use these names when more critical determination has been either impossible or unnecessary. It is most important that *when a binary is thus used in an inclusive sense the abbreviation* agg. *must follow the name.*

Binary names for known or presumed hybrids have for the most part been excluded, both because there is so often uncertainty as to their application and because the principles underlying the nomenclature of hybrids and hybrid swarms are so badly in need of reconsideration. Exceptions have been made, however, of the numerous putative hybrids in the genus *Potamogeton*, and of certain hybrid grasses.

The names recommended are as far as possible in accordance with the International Rules of Botanical Nomenclature. The authorities for names are cited in conventionally abbreviated forms. When names have been proposed but not published by one author and subsequently published and ascribed to him by another author, the name of the publishing author alone has been appended. Thus *Spergularia bocconi* (Scheele) Foucaud ex Merino is cited simply as *S. bocconi* (Scheele) Merino. When, on the other hand, the description has been supplied by one author though published in the work of another author, only the describing author's name is cited. Thus *Oenothera lamarkiana* Seringe in DC. is cited as *O. lamarkiana* Ser. Except in *Potamogeton* no attempt has been made to supply a full synonymy. Familiar synonyms are placed in brackets after the recommended names, but are included merely for information and must not be regarded as alternatives to the recommended names.

Long-established names are retained, even when known to be invalid, in certain instances

where there is still doubt as to the correct name under the Rules. Thus *Torilis anthriscus* (L.) Gmel. is an illegitimate combination for the plant commonly known by that name, but it is not yet certain that it should be replaced by *T. japonica* (Houtt.) DC., and its continued use is therefore recommended.

Names preceded by a dagger (†) also appear to need revision for nomenclatural or taxonomic reasons, but must be used until investigations have been completed.

Besides undoubted British natives the List includes naturalized aliens and some commonly encountered casuals. The intention has been to mark all such species with an asterisk, but it must be repeated that the List should not be regarded as expressing a deeply considered and authoritative opinion either on the claims of species for inclusion or on the status of certain border-line cases.

The sequence of species, genera and families is usually that of the London Catalogue, as a matter of convenience and because it is not intended that the List should impose any taxonomic system or concepts. It has, nevertheless, seemed desirable to depart from past British usage in the delimitation of certain families and genera, and to follow instead established Continental practice or recent monographers.

Lists of British Rubi and Hieracia (kindly provided by Mr Wm. Watson and Mr H. W. Pugsley respectively) have been added as appendices to the main List. Since both these lists have been based largely on unpublished work and include many new names, it has seemed desirable to print them in a different way from the rest of the List, naming the subgeneric divisions recognized by their compilers. The list of Rubi includes also a fuller synonymy and references to figures. It is felt very strongly that the treatment of these two difficult genera needs careful reconsideration in the interests of the student of vegetation. Binary names should be restricted to more broadly defined aggregates than at present, and adequate keys should enable the worker to press his identification beyond *Rubus fruticosus* agg. or *Hieracium* sp. to a point which gives him and his readers some clearer idea of the nature of the plants encountered, but which does not demand the hopeless search for identity with one of the hundreds of described 'species'. Our imperfect knowledge of the status of the entities included in the two genera does not make this an easy task at present, but it is clearly something to be aimed at in the near future, and something that may in time be achieved by the co-operation of taxonomists with ecologists, geneticists and cytologists.

It is fully realized that this Check List could have been greatly improved had much more time been expended on its preparation. Bibliographical research, severely restricted during the war, will soon become more easily possible; and further observations and experiments might readily clarify a number of obscurities and lead to a more consistent treatment of many comparatively neglected genera. But there would always be much more left to be done, and meanwhile there is urgent need for a List. There seems, therefore, a strong case for the immediate publication of one which summarizes information already available and which may be kept up to date by periodic revision.

The List could not have been prepared without the collaboration of many specialists, whose help is now most gratefully acknowledged. Besides Dr N. V. Polunin, Dr W. B. Turrill and Mr A. J. Wilmott (Advisory Taxonomists to the Biological Flora), special mention must be made of Mr J. P. M. Brenan, Mr J. E. Dandy, Mr H. W. Pugsley and Mr T. G. Tutin, who have given their time unsparingly in supplying invaluable information and expert advice. Thanks are also due to the following for help with the groups specified:

Mr R. W. Butcher (*Thalictrum* and *Ranunculus*), Mr J. E. Dandy (Alismataceae, Hydrocharitaceae, Butomaceae, Scheuchzeriaceae, Aponogetonaceae, Zosteraceae, Najadaceae), Mr J. E. Dandy and Dr G. Taylor (*Potamogeton* and *Ruppia*), Prof. J. Heslop Harrison (*Rosa, Salix, Orchis*), Dr W. O. Howarth (*Festuca*), Mr C. E. Hubbard (Gramineae), Dr R. Melville (*Ulmus*), Mr E. Nelmes (*Carex*), Mr H. W. Pugsley (*Fumaria, Euphrasia, Hieracium*), Dr P. W. Richards (Juncaceae), Mr V. S. Summerhayes (Orchidaceae), Dr E. F. Warburg (*Gentiana, Sorbus*), and Mr W. Watson (*Rubus*). It should be added that these specialists cannot be held responsible for all views implied in the form and content of parts of the List which have been drawn up with their help.

1 *May* 1946.

CHECK LIST OF BRITISH VASCULAR PLANTS

RANUNCULACEAE

Clematis L.
  C. vitalba L.

Thalictrum L.
  T. alpinum L.
  T. minus agg.
    T. arenarium Butcher (T. dunense auct. angl.)
    T. babingtonii Butcher
    T. montanum Wallr.
    T. collinum Wallr. (T. flexuosum auct. angl.)
    T. capillare Rchb. (T. kochii auct. angl.)
    T. majus Crantz
    T. umbrosum Butcher
    T. expansum Jord. (T. pubescens auct. angl.)
  T. flavum L.

Anemone L.
  A. pulsatilla L.
  A. nemorosa L.
  *A. ranunculoides L.
  *A. apennina L.

Adonis L.
  *A. annua L. (A. autumnalis L.)

Myosurus L.
  M. minimus L.

Ranunculus L.
  R. circinatus Sibth.
  R. fluitans Lam.
  R. trichophyllus Chaix (R. divaricatus Schrank)
    R. drouetii F. Schultz (? R. paucistamineus Tausch)
  R. heterophyllus Weber
    R. radians Revel
  R. peltatus Schrank (incl. R. floribundus Bab. and R. penicillatus Bab.)
  R. pseudofluitans Baker & Foggitt
  R. sphaerospermus Boiss. & Blanche
  R. baudotii Godr.
  R. tripartitus DC.
  R. lutarius (Revel) Bouvet (R. intermedius auct. angl.)
  R. lenormandi F. Schultz
  R. hederaceus L.
  R. sceleratus L.

  R. ophioglossifolius Vill.
  R. flammula L.
    R. scoticus E. S. Marshall
  R. reptans L.
  R. lingua L.
  R. auricomus L.
  R. acris L.
  R. repens L.
  R. bulbosus L.
  R. sardous Crantz (R. hirsutus Curt.)
  R. parviflorus L.
  R. arvensis L.
  R. flabellatus Desf.
  R. ficaria L.

Caltha L.
  C. palustris L.
    C. radicans T. F. Forst.

Trollius L.
  T. europaeus L.

Helleborus L.
  H. viridis L.
  H. foetidus L.

Eranthis Salisb.
  *E. hyemalis (L.) Salisb.

Aquilegia L.
  A. vulgaris L.
  *A. pyrenaica DC. (A. alpina auct. angl.)

Nigella L.
  *N. damascena L.

Delphinium L.
  *D. gayanum Wilmott (D. ajacis auct. angl.)
  *D. consolida L.

Aconitum L.
  A. anglicum Stapf (A. napellus auct. angl.)

Actaea L.
  A. spicata L.

Paeonia L.
  *P. corallina Retz. (P. mascula Desf., non Mill.)

BERBERIDACEAE

Berberis L.
 B. vulgaris L.

Mahonia Nutt.
 *M. aquifolium (Pursh) Nutt. (Berberis aquifolium Pursh)

Epimedium L.
 *E. alpinum L.

NYMPHAEACEAE

Nuphar Sm.
 N. lutea (L.) Sm.
 N. pumila (Timm) DC.

Nymphaea L.
 N. alba L.
 N. occidentalis (Ostenf.) Moss

PAPAVERACEAE

Papaver L.
 *P. somniferum L.
 P. rhoeas L.
 P. dubium L.
 P. lecoqii Lamotte
 P. argemone L.
 P. hybridum L.

Meconopsis Vig.
 M. cambrica (L.) Vig.

Glaucium Mill.
 G. flavum Crantz (G. luteum Scop.)

Roemeria Medic.
 *R. hybrida (L.) DC.

Chelidonium L.
 *C. majus L.

FUMARIACEAE

Corydalis Medic.
 *C. lutea (L.) DC.
 *C. bulbosa (L.) DC. (C. solida (L.) Sw.)
 C. claviculata (L.) DC.

Fumaria L.
 F. occidentalis Pugsl.
 F. capreolata L.
 F. purpurea Pugsl.
 F. bastardii Bor.
 F. martinii Clavaud
 F. muralis agg.
  F. muralis Koch
  F. neglecta (Pugsl.) Pugsl.
  F. boraei Jord.
 F. micrantha Lag.
 F. officinalis L.
 F. vaillantii Lois.
 F. parviflora Lam.

CRUCIFERAE

Matthiola R.Br.
 M. sinuata (L.) R.Br.
 M. incana (L.) R.Br.

Cheiranthus L.
 *C. cheiri L.

Nasturtium R.Br.
 N. officinale R.Br.
 N. uniseriatum Howard and Manton

Rorippa Scop.
 R. sylvestris (L.) Besser (Nasturtium sylvestre (L.) R.Br.)
 R. islandica (Oeder) Borbás (Nasturtium palustre (Leyss.) DC.)
 R. amphibia (L.) Besser (Nasturtium amphibium (L.) R.Br.)
 *R. austriaca (Crantz) Besser

Barbarea B.Ehrh.
 B. vulgaris R.Br.
  B. arcuata (Presl) Rchb.
 B. stricta Andrz.
 *B. intermedia Bor.
 *B. verna (Mill.) Aschers. (B. praecox (Sm.) R.Br.)

Arabis L.
 A. alpina L.
 A. petraea (L.) Lam.
 A. stricta Huds. (A. scabra All.)
 A. brownii Jord. (A. hibernica Wilmott, A. ciliata auct.)
 A. hirsuta (L.) Scop.
 *A. turrita L.
 *A. caucasica Willd. (A. albida Stev.)

Turritis L.
 T. glabra L. (Arabis glabra (L.) Bernh.)

Cardamine L.
 C. amara L.
 C. pratensis L.
 C. hirsuta L.
 C. flexuosa With.
 C. impatiens L.
 *C. trifolia L.

Dentaria L.
 D. bulbifera L. (Cardamine bulbifera (L.) Crantz)

Alyssum L.
 *A. alyssoides (L.) L. (A. calycinum L.)

Lobularia Desv.
 *L. maritima (L.) Desv. (Alyssum maritimum (L.) Lam.)

Berteroa DC.
 *B. incana (L.) DC. (Alyssum incanum L.)

Draba L.
 D. muralis L.
 D. incana L.
 D. rupestris R.Br.
 D. aizoides L.

Erophila DC.
 E. verna (L.) Chevall. (Draba verna L.)
  E. spathulata Lang (E. boerhavii (Van Hall) Dum., incl. E. inflata (Hook. f.) Wats.).
  E. praecox (Stev.) DC.

Cochlearia L.
 C. officinalis L.
 C. alpina Wats.
 C. micacea E. S. Marshall (C. arctica auct.)
 C. danica L.
 C. scotica Druce (C. groenlandica auct.)
 C. anglica L.

Armoracia Gilib.
 *A. lapathifolia Gilib. (Cochlearia armoracia L.)

Malcolmia R.Br.
  *M. maritima (L.) R.Br.

Hesperis L.
  *H. matronalis L.

Arabidopsis Heynh.
  A. thaliana (L.) Heynh. (Sisymbrium thalianum
    (L.) Gay)

Sisymbrium L.
  S. officinale (L.) Scop.
  *S. altissimum L. (S. pannonicum Jacq.)
  *S. orientale L. (S. columnae Jacq.)
  *S. irio L.
  *S. strictissimum L.

Descurainia Webb & Berth.
  D. sophia (L.) Prantl (Sisymbrium sophia L.)

Alliaria B. Ehrh.
  A. petiolata (Bieb.) Cavara & Grande (Sisymbrium
    alliaria (L.) Scop , A. officinalis Bieb.)

Erysimum L.
  E. cheiranthoides L.

Conringia Adans.
  *C. orientalis (L.) Dum. (Erysimum orientale (L.)
    R.Br., non Mill., E. perfoliatum Crantz)

Camelina Crantz
  *C. sativa (L.) Crantz
  *C. sylvestris Wallr.

Subularia L.
  S. aquatica L.

Brassica L.
  B. oleracea L.
  *B. napus L. (incl. B. napobrassica Mill.)
  *B. campestris L. (incl. B. rapa L.)
  B. nigra (L.) Koch

Brassicella Fourr.
  B. monensis (L.) O. E. Schulz
  B. erucastrum (L.) O. E. Schulz (B. cheiranthos
    (Vill.) Pugsl.)
  B. wrightii O. E. Schulz

Hirschfeldia Moench
  H. incana (L.) Lagrèze-Fossat (Brassica adpressa
    Boiss.)

Sinapis L.
  S. arvensis L. (Brassica arvensis (L.) Kuntze, non L.)
  *S. alba L. (Brassica alba (L.) Boiss., non Gilib.)

Erucastrum (DC.) C. Presl
  *E. gallicum (Willd.) O. E. Schulz

Diplotaxis DC.
  D. tenuifolia (L.) DC.
  D. muralis (L.) DC.
  *D. erucoides (L.) DC.

Capsella Medic.
  C. bursa-pastoris (L.) Medic.

Coronopus Boehm.
  C. squamatus (Forsk.) Aschers. (C. procumbens
    Gilib., Senebiera coronopus (L.) Poir.)
  *C. didymus (L.) Sm. (Senebiera didyma (L.) Pers.)

Lepidium L.
  L. latifolium L.
  *L. ruderale L.
  *L. graminifolium L.
  *L. neglectum Thell.
  *L. sativum L.
  L. campestre (L.) R.Br.
  L. smithii Hook. (L. heterophyllum var. canescens
    Gren. & Godr.)

Cardaria Desv.
  *C. draba (L.) Desv. (Lepidium draba L.)

Thlaspi L.
  *T. arvense L.
  T. perfoliatum L.
  T. alpestre L.
    T. calaminare Lej. & Court. (T. virens Jord.)

Iberis L.
  I. amara L.

Teesdalia R.Br.
  T. nudicaulis (L.) R.Br.
  T. coronopifolia (Berg.) Thell. (T. lepidium DC.)

Hornungia Rchb.
  H. petraea (L.) Rchb. (Hutchinsia petraea (L.)
    R.Br.)

Isatis L.
  *I. tinctoria L.

Bunias L.
  *B. erucago L.
  *B. orientalis L.

Crambe L.
  C. maritima L.

Cakile Mill.
  C. maritima Scop.

Rapistrum Crantz
  *R. perenne (L.) All.
  *R. rugosum (L.) All.

Raphanus L.
  R. raphanistrum L.
  R. maritimus Sm.

RESEDACEAE
Reseda L.
  *R. alba L.
  R. lutea L.
  *R. stricta Pers.
  R. luteola L.
  *R. phyteuma L.

CISTACEAE
Helianthemum Mill.
  H. guttatum (L.) Mill.
  H. canum (L.) Baumg.
  †H. nummularium (L.) Mill. (H. chamaecistus Mill.,
    H. vulgare Gaertn.)
  †H. polifolium Mill. (? H. apenninum (L.) Mill.)

VIOLACEAE

Viola L.

V. odorata L.
V. hirta L.
V. calcarea (Bab.) Greg.
V. palustris L.
†V. juressi K. Wein (V. epipsila auct. angl., non Ledeb.)
V. reichenbachiana Bor. (V. sylvestris auct.)
V. riviniana Rchb.
V. rupestris Schmidt
V. canina L.
†V. montana auct., ? L.
V. lactea Sm.
V. stagnina Kit. (? V. persicifolia Roth)
V. arvensis agg.
  V. agrestis Jord.
  V. segetalis Jord.
  V. obtusifolia Jord.
  V. latifolia Drabble
  V. ruralis Bor.
  V. deseglisei Bor.
  V. anglica Drabble
  V. arvatica Jord.
  V. derelicta Jord.
V. tricolor agg.
  V. contempta Jord.
  V. variata Jord.
  V. cantiana Drabble
  V. monticola Jord.
  †V. alpestris (DC.) Jord., non Hegetschw.; nom. illegit.
  V. lejeunii Jord.
  V. lloydii Bor.
  V. orcadensis Drabble
V. lepida Jord.
V. lutea Huds.
  V. curtisii E. Forst.
  V. pesneaui Lloyd
V. nana (DC.) Corbière

POLYGALACEAE

Polygala L.

P. vulgaris L.
P. oxyptera Rchb. (P. dubia Bellynck)
P. serpyllifolia Hose (P. serpyllacea Weihe)
P. calcarea F. Schultz
P. amara L. (P. amarella Crantz)
P. austriaca Crantz

FRANKENIACEAE

Frankenia L.

F. laevis L.

CARYOPHYLLACEAE

Dianthus L.

D. armeria L.
D. deltoides L.
D. gratianopolitanus Vill. (D. caesius Sm., D. glaucus auct.)
*D. gallicus Pers.
*D. plumarius L.
*D. caryophyllus L.

Kohlrauschia Kunth

K. prolifera (L.) Kunth (Dianthus prolifer L., Tunica prolifera (L.) Scop.)

Saponaria L.

*S. officinalis L.

Silene L.

S. cucubalus Wibel (S. inflata Sm.)
†S. angustifolia (Ten.) Guss., non Poir.
S. maritima (Hornem.) With.
S. conica L.
*S. conoidea L.
S. gallica agg.
  S. gallica L.
  S. anglica L.
  S. quinquevulnera L.
S. acaulis (L.) Jacq.
S. otites (L.) Wibel
S. nutans L. (incl. S. dubia Rohrb.)
*S. italica (L.) Pers.

Cucubalus L.

*C. baccifer L.

Melandrium Roehl.

M. noctiflorum (L.) Fr. (Silene noctiflora L.)
M. album (Mill.) Garcke (Lychnis alba Mill.)
M. dioicum (L.) Coss. & Germ. (Lychnis dioica L., L. diurna Sibth.)

Lychnis L.

L. flos-cuculi L.

Viscaria Bernh.

V. vulgaris Bernh. (Lychnis viscaria L.)
V. alpina (L.) Don (Lychnis alpina L.)

Agrostemma L.

A. githago L. (Lychnis githago (L.) Scop.)

Holosteum L.

H. umbellatum L.

Cerastium L.

C. tetrandrum Curt.
  C. subtetrandrum (Lange) Murb.
C. pumilum Curt.
C. semidecandrum L.
C. viscosum L. (C. glomeratum Thuill.)
C. vulgatum L. (C. triviale Link)
C. alpinum L.
C. edmondstonii (Edmondst.) Murb. & Ostenf. (C. arcticum auct.)
C. arvense L.
C. cerastoides (L.) Britton (C. trigynum Vill.)

Moenchia Ehrh.

M. erecta (L.) Gaertn., Mey. and Scherb.

Myosoton Moench

M. aquaticum (L.) Moench (Stellaria aquatica (L.) Scop., Malachium aquaticum (L.) Fr.)

Stellaria L.

S. nemorum L.
S. media (L.) Vill.
S. apetala Ucria (incl. S. pallida (Dum.) Piré and S. boraeana Jord.)
S. neglecta Weihe (S. umbrosa auct.)
  S. elisabethae F. Schultz
S. holostea L.
S. palustris Retz. (incl. S. dilleniana Moench and S. glauca With.)
S. graminea L.
S. alsine Grimm (S. uliginosa Murr.)

Arenaria L.
  A. verna L.
  A. rubella (Wahlenb.) Sm.
  A. uliginosa Schlecht. (Minuartia stricta (Sw.) Hiern)
  A. tenuifolia L.
  A. trinervia L.
  A. serpyllifolia L.
  A. leptoclados (Rchb.) Guss.
  A. ciliata L.
  A. gothica Fr.
  A. norvegica Gunn.
  A. peploides L. (Honckenya peploides (L.) Ehrh.)
  A. sedoides (L.) F. J. Hanb. (Cherleria sedoides L.)

Sagina L.
  S. maritima Sm.
  S. apetala Ard.
  S. ciliata Fr. (incl. S. reuteri Boiss.)
    S. filicaulis Jord.
  S. procumbens L.
  S. boydii F.B. White
  S. saginoides (L.) Karst. (S. linnei C. Presl)
    S. scotica (Druce) Druce
  S. intermedia Fenzl (S. caespitosa auct.. angl. S. nivalis Fr.)
  S. subulata (Sw.) C. Presl
  S. nodosa (L.) Fenzl

Spergula L.
  S. arvensis L. (S. vulgaris Boenn.)
  S. sativa Boenn.

Spergularia J. & C. Presl
  S. rubra (L.) J. & C. Presl
  S. bocconi (Scheele) Merino (S. atheniensis Aschers., S. campestris Willk., non Aschers.)
  S. salina J. & C. Presl
  S. marginata (DC.) Kittel (S. media auct.)
  S. rupicola Lebel (S. rupestris Lebel, non Cambess.)

Polycarpon L.
  P. tetraphyllum (L.) L.

PORTULACACEAE
Claytonia L.
  *C. alsinoides Sims
  *C. perfoliata Willd.

Montia L.
  M. verna Neck. (M. chondrosperma Fenzl)
    M. rivularis C. C. Gmel.
  M. fontana L. (incl. M. lamprosperma Cham.)

TAMARICACEAE
Tamarix L.
  *T. gallica L.

ELATINACEAE
Elatine L.
  E. hexandra (Lapierre) DC.
  E. hydropiper L.

HYPERICACEAE
Hypericum L.
  H. androsaemum L.
  *H. hircinum L.
  *H. elatum Ait.
  *H. calycinum L.
  H. perforatum L.

H. dubium Leers (H. quadrangulum auct.)
H. quadrangulum L. (H. tetrapterum Fr.)
H. undulatum Willd.
H. humifusum L.
H. linarifolium Vahl
H. pulchrum L.
H. hirsutum L.
H. montanum L.
H. elodes L.

MALVACEAE
Althaea L.
  A. officinalis L.
  *A. hirsuta L.

Lavatera L.
  L. arborea L.
  *L. cretica L. (L. sylvestris Brot.)

Malva L.
  M. moschata L.
  M. sylvestris L.
  M. neglecta Wallr. (M. rotundifolia auct.)
  *M. rotundifolia L. (M. pusilla Sm.)
  *M. parviflora L.

TILIACEAE
Tilia L.
  T. platyphyllos Scop.
  *T. vulgaris Hayne ?of hybrid origin
  T. cordata Mill.

LINACEAE
Radiola Hill
  R. linoides Roth

Linum L.
  L. catharticum L.
  L. anglicum Mill. (L. perenne auct. angl.)
  L. bienne Mill. (L. angustifolium Huds.)

GERANIACEAE
Geranium L.
  G. sanguineum L.
  *G. versicolor L. (G. striatum L.)
  *G. nodosum L.
  *G. phaeum L.
  G. sylvaticum L.
  G. pratense L.
  *G. endressi Gay
  G. pyrenaicum Burm. f.
  G. molle L.
  G. pusillum L.
  G. rotundifolium L.
  G. dissectum L.
  G. columbinum L.
  G. lucidum L.
  G. robertianum L.
  G. purpureum Vill.

Erodium L'Hérit.
  E. cicutarium agg.
    E. cicutarium (L.) Ait.
    E. triviale Jord.
    E. pimpinellifolium (Cav.) Sibth.
    E. ballii Jord.
    E. lebelii Jord.
    E. neglectum Baker f. & Salmon
    E. glutinosum Dum.
  E. moschatum (L.) Ait.
  E. maritimum (L.) Ait.

OXALIDACEAE

Oxalis L.

O. acetosella L.
*O. corniculata L.
*O. stricta L.

BALSAMINACEAE

Impatiens L.

I. noli-tangere L.
*I. capensis Meerburgh (I. biflora Walt., I. fulva Nutt.)
*I. parviflora DC.
*I. glandulifera Royle (I. roylei Walp.)

AQUIFOLIACEAE

Ilex L.

I. aquifolium L.

CELASTRACEAE

Euonymus L.

E. europaeus L.

RHAMNACEAE

Rhamnus L.

R. cathartica L.

Frangula Mill.

F. alnus Mill. (Rhamnus frangula L.)

ACERACEAE

Acer L.

*A. pseudo-platanus L.
A. campestre L.
*A. platanoides L.

HIPPOCASTANACEAE

Aesculus L.

*A. hippo-castanum L.

LEGUMINOSAE

Lupinus L.

*L. nootkatensis Sims
*L. arboreus Sims

Laburnum Medic.

*L. anagyroides Medic. (Cytisus laburnum L.)

Genista L.

G. anglica L.
G. pilosa L.
G. tinctoria L.

Ulex L.

U. europaeus L.
U. gallii Planch.
U. minor Roth (U. nanus Forst.)

Sarothamnus Wimmer

S. scoparius (L.) Koch (Cytisus scoparius (L.) Link)

Ononis L.

O. repens L.
O. spinosa L.
O. reclinata L.

Trigonella L.

T. ornithopodioides (L.) DC.

Medicago L.

*M. sativa L.
× M. varia Martyn (incl. M. sylvestris Fr.)
M. falcata L.
M. lupulina L.
M. hispida Gaertn.
   M. denticulata Willd.
   *M. apiculata Willd.
   *M. lappacea Desr.
M. arabica (L.) Huds. (M. maculata Sibth.)
M. minima (L.) Bartal.

Melilotus Mill.

M. altissima Thuill.
*M. alba Medic.
*M. officinalis (L.) Lam. (M. arvensis Wallr.)
*M. indica (L.) All.

Trifolium L.

T. subterraneum L.
T. pratense L.
T. medium L.
T. ochroleucon Huds.
T. squamosum L. (T. maritimum Huds.)
*T. incarnatum L.
T. molinerii Balb.
*T. stellatum L.
T. arvense L.
T. bocconi Savi
T. striatum L.
T. scabrum L.
T. glomeratum L.
T. suffocatum L.
T. strictum L.
*T. hybridum L.
T. repens L.
T. fragiferum L.
*T. resupinatum L.
*T. agrarium L.
T. campestre Schreb. (T. procumbens auct.)
T. dubium Sibth.
T. filiforme L.

Anthyllis L.

A. vulneraria L. (incl. A. dillenii Schult. (A. rubra Gouan) and A. maritima Schweigg.)

Lotus L.

L. corniculatus L.
L. tenuis Willd.
L. uliginosus Schkuhr (L. major auct.)
L. angustissimus L.
L. hispidus DC.

Tetragonolobus Scop.

*T. siliquosus (L.) Roth

Galega L.

*G. officinalis L.

Robinia L.

*R. pseudo-acacia L.

Astragalus L.

A. alpinus L.
A. danicus Retz.
A. glycyphyllos L.
*A. boeticus L.

Oxytropis DC.

O. halleri Bunge (O. sericea (Lam.) Simonk., O. uralensis auct.)
O. campestris (L.) DC.

Coronilla L.
*C. varia L.

Ornithopus L.
O. perpusillus L.

Artrolobium Desv.
A. pinnatum (Mill.) Britten & Rendle (Ornithopus ebracteatus Brot.)

Hippocrepis L.
H. comosa L.

Onobrychis Mill.
O. viciifolia Scop. (O. sativa Lam.)

Vicia L.
V. hirsuta (L.) S. F. Gray
V. tetrasperma (L.) Schreb.
V. tenuissima (Bieb.) Schinz & Thell. (V. gracilis Lois.)
V. cracca L.
V. orobus DC.
V. sylvatica L.
V. sepium L.
V. lutea L.
*V. hybrida L.
*V. sativa L.
V. angustifolia L.
V. lathyroides L.
V. bithynica (L.) L.

Lathyrus L.
L. aphaca L.
L. nissolia L.
*L. hirsutus L.
L. pratensis L.
L. tuberosus L.
L. sylvestris L.
L. palustris L.
L. japonicus Willd. (incl. L. maritimus Bigel.)
L. montanus Bernh.
L. niger (L.) Bernh.

ROSACEAE

Prunus L.
P. spinosa L.
P. insititia L.
*P. domestica L.
*P. cerasifera Ehrh.
P. avium L.
P. cerasus L.
P. padus L.
*P. laurocerasus L.

Spiraea L.
*S. salicifolia L.

Filipendula B. Ehrh.
F. ulmaria (L.) Maxim. (Spiraea ulmaria L.)
F. hexapetala Gilib. (Spiraea filipendula L.)

Rubus L.
See list provided by Mr Wm. Watson on p. 337.

Dryas L.
D. octopetala L.

Geum L.
G. urbanum L.
G. rivale L.

Fragaria L.
F. vesca L.
*F. moschata Duchesne (F. elatior Ehrh.)
*F. chiloensis Duchesne

Potentilla L.
*P. norvegica L.
P. sterilis (L.) Garcke (P. fragariastrum Ehrh.)
P. verna L.
P. crantzii (Crantz) Beck (P. maculata Pourr., non Gilib., P. alpestris Hall. f.)
P. erecta (L.) Räusch (P. tormentilla Neck.)
P. procumbens Sibth.
P. reptans L.
P. anserina L.
P. rupestris L.
P. argentea L.
*P. recta L.
P. fruticosa L.

Comarum L.
C. palustre L. (Potentilla palustris (L.) Scop.)

Sibbaldia L.
S. procumbens L. (Potentilla sibbaldi Hall. f.)

Alchemilla L.
A. arvensis (L.) Scop.
A. vulgaris L., sp. agg.
A. minor Huds.) (A. hybrida Mill., A. pubescens auct., ? Lam.)
A. xanthochlora Rothm. (A. pratensis auct., ? Schmidt)
A. curtiloba Buser
A. vestita (Buser) Raunk. (A. anglica Rothm.; A. pseudominor Wilmott, A. minor auct.)
A. filicaulis Buser
A. pastoralis Buser (? A. monticola Opiz)
A. subcrenata Buser
A. tenuis Buser
A. glabra Neygenfind (A. alpestris auct., ? Schmidt)
A. acutidens Buser
A. glomerulans Buser
A. reniformis Buser
A. connivens Buser
A. firma Buser
A. salmoniana Jaquet
A. colorata Buser
A. coriacea Buser
A. crinita Buser
A. conjuncta Bab. (A. argentea Don, non Lam.)
A. alpina L.

Agrimonia L.
A. eupatoria L.
A. odorata (Gouan) Mill.
*A. agrimonoides L.

Acaena L.
*A. anserinifolia (J. R. & G. Forst.) Druce (A. sanguisorbae Vahl)

Poterium L.
P. sanguisorba L.
*P. polygamum Waldst. & Kit.

Sanguisorba L.
S. officinalis L.

Rosa L.

R. arvensis Huds.
R. stylosa Desv. agg.
R. spinosissima L. (incl. R. pimpinellifolia L. and R. rubella Sm.)
R. canina L. agg.
R. dumetorum Thuill. agg.
R. afzeliana Fr. agg. (? R. dumalis Bechst., R. glauca Vill., non Pourr.)
R. caesia Sm. agg. (R. coriifolia Fr.)
R. obtusifolia Desv. agg. (R. tomentella Léman)
R. villosa L. agg. (incl. R. pomifera Herm. and R. mollis Sm.)
R. sherardi Davies agg. (incl. R. omissa Déségl. and R. hurstiana Harrison)
R. tomentosa Sm. agg.
R. rubiginosa L. agg.
R. micrantha Sm. agg.
R. elliptica Tausch agg.
R. agrestis Savi agg.

Sorbus L.

*S. domestica L.
S. aucuparia L.
S. intermedia agg.
†S. fennica Hedl. et auct. angl., non Fr.
S. arranensis Hedl.
S. leyana Wilmott
S. minima (Ley) Hedl.
*S. intermedia (Ehrh.) Pers. (S. scandica Fr.)
S. anglica Hedl.
S. aria agg.
S. aria (L.) Crantz
S. rupicola (Syme) Hedl.
S. porrigens Hedl.
S. latifolia agg.
S. latifolia (Lam.) Pers.
S. bristoliensis Wilmott
S. vagensis Wilmott
S. subcuneata Wilmott
S. torminalis (L.) Crantz

Pyrus L.

*P. communis L.
P. cordata Desv.

Malus Mill.

M. pumila Mill. (Pyrus malus L., p.p.)

Mespilus L.

*M. germanica L.

Crataegus L.

C. oxyacanthoides Thuill. (C. oxyacantha auct.)
C. monogyna Jacq.

Cotoneaster B. Ehrh.

C. integerrima Medic.
*C. microphylla Lindl.
*C. simonsii Baker

SAXIFRAGACEAE

Saxifraga L.

S. oppositifolia L.
S. nivalis L.
S. stellaris L.
S. geum L. (S. hirsuta auct., non L.) ? of hybrid origin
S. hirsuta L. (S. geum auct., non L.) ? of hybrid origin
S. umbrosa L.
S. spathularis Brot. (S. umbrosa auct., non L.)
S. lactiflora Pugsl. (S. geum auct., non L.)
S. hirculus L.

S. aizoides L.
S. tridactylites L.
S. rivularis L.
S. cernua L.
S. granulata L.
S. cespitosa agg.
S. cespitosa L. (incl. S. groenlandica L.)
S. incurvifolia D. Don
S. sternbergii Willd.
S. rosacea Moench (S. decipiens Ehrh., S. palmata Sm.)
S. sponhemica C. C. Gmel.
S. hirta Sm. (S. hibernica Haw.)
S. platypetala Sm.
S. drucei E. S. Marshall
S. affinis D. Don
S. laetevirens D. Don
S. elongella Sm., non Haw.
S. hypnoides agg.
S. hypnoides L.
S. angustifolia Haw.
†S. spathulata Haw., non Desf.: nom. illegit.
S. viscosa Haw.
S. recurva Schleich.
S. leptophylla D. Don (?S. leptophylla Pers.; if not, nom. illegit.)

Chrysosplenium L.

C. oppositifolium L.
C. alternifolium L.

PARNASSIACEAE

Parnassia L.

P. palustris L.

GROSSULARIACEAE

Ribes L.

*R. uva-crispa L. (incl. R. grossularia L.)
R. alpinum L.
R. rubrum agg.
*R. rubrum L. (R. vulgare Schneider, R. domesticum Jancz.)
R. spicatum Robs. (R. petraeum Sm., non Wulf.)
R. nigrum L.

CRASSULACEAE

Tillaea L.

T. muscosa L.
T. aquatica L.

Umbilicus DC.

U. pendulinus DC. (Cotyledon umbilicus-veneris L.)

Sedum L.

S. rosea (L.) Scop.
S. telephium L. (S. purpureum Link)
S. fabaria Koch
*S. dasyphyllum L.
S. anglicum Huds.
*S. album L.
*S. micranthum DC.
S. acre L.
*S. sexangulare L.
S. rupestre L.
S. forsterianum Sm.
*S. reflexum L.
S. villosum L.

Sempervivum L.

*S. tectorum L.

DROSERACEAE

Drosera L.
 D. rotundifolia L.
 D. anglica Huds.
 D. longifolia L. (D. intermedia Drev. & Hayne)

HALORAGACEAE

Hippuris L.
 H. vulgaris L.

Myriophyllum L.
 M. verticillatum L.
 M. spicatum L.
 M. alterniflorum DC.

CALLITRICHACEAE

Callitriche L.
 C. palustris L. (C. verna L., C. vernalis Koch)
 C. stagnalis Scop.
 C. polymorpha Loennr.
 C. intermedia Hoffm. (C. hamulata Koch)
  C. pedunculata DC.
 C. obtusangula Le Gall.
 C. autumnalis L.
 C. truncata Guss.

LYTHRACEAE

Peplis L.
 P. portula L.

Lythrum L.
 L. salicaria L.
 L. hyssopifolia L.

ONAGRACEAE

Chamaenerion Adans.
 C. angustifolium (L.) Scop. (Epilobium augusti-
 folium L.)

Epilobium L.
 E. hirsutum L.
 E. parviflorum Schreb.
 E. montanum L.
 E. lanceolatum Seb. & Maur.
 E. roseum Schreb.
 *E. adenocaulon Hausskn.
 E. tetragonum L.
 E. obscurum Schreb.
 E. lamyi F. Schultz
 E. palustre L.
 E. alsinifolium Vill.
 E. alpinum L. (E. anagallidifolium Lam.)
 *E. nummularifolium A. Cunn.
 *E. pedunculare A. Cunn.

Ludwigia L.
 L. palustris (L.) Elliott

Oenothera L.
 *O. biennis L.
 *O. ammophila Focke
 *O. lamarkiana Ser.
 *O. stricta Ledeb. (O. odorata Jacq.)

Fuchsia L.
 *F. magellanica Lam.

Circaea L.
 C. lutetiana L.
 C. intermedia Ehrh.
 C. alpina L.

CUCURBITACEAE

Bryonia L.
 B. dioica Jacq.

AIZOACEAE

Carpobrotus N.E. Br.
 *C. edulis (L.) N.E. Br. (Mesembryanthemum
 edule L.)

UMBELLIFERAE

Hydrocotyle L.
 H. vulgaris L.

Eryngium L.
 E. maritimum L.
 E. campestre L.

Astrantia L.
 *A. major L.

Sanicula L.
 S. europaea L.

Danaa All.
 D. cornubiensis (L.) Burnat (Physospermum cornu-
 biense (L.) DC.)

Conium L.
 C. maculatum L.

Smyrnium L.
 *S. olusatrum L.

Bupleurum L.
 *B. fruticosum L.
 B. rotundifolium L.
 B. opacum (Ces.) Lange (B. aristatum auct.)
 B. tenuissimum L.
 B. falcatum L.

Trinia Hoffm.
 T. glauca (L.) Dum.

Apium L.
 A. graveolens L.
 A. nodiflorum (L.) Lag.
 A. repens (Jacq.) Lag.
 A. inundatum (L.) Rchb. f.
 A. moorei (Syme) Druce ? of hybrid origin

Cicuta L.
 C. virosa L.

Ammi L.
 *A. majus L.

Carum L.
 C. verticillatum (L.) Koch
 *C. carvi L.

Petroselinum Hill
 *P. crispum (Mill.) Nym. (P. sativum Hoffm., Carum
 petroselinum (L.) Benth.)
 P. segetum (L.) Koch (Carum segetum (L.) Hook. f.)

Bunium L.
 B. bulbocastanum L. (Carum bulbocastanum (L.)
 Koch)

Sison L.
 S. amomum L.

Falcaria Host
*F. vulgaris Bernh.

Sium L.
S. latifolium L.
S. erectum Huds. (S. angustifolium L.)

Aegopodium L.
*A. podagraria L.

Pimpinella L.
P. saxifraga L.
P. major (L.) Huds. (P. magna L.)

Conopodium Koch
C. majus (Gouan) Lor. & Barr. (C. denudatum Koch)

Myrrhis Mill.
M. odorata (L.) Scop.

Chaerophyllum L.
C. temulum L.
*C. aureum L.

Scandix L.
S. pecten-veneris L.

Anthriscus Pers.
A. scandicina (Weber) Mansf. (A. vulgaris Pers., non Bernh.; A. scandix (Scop.) Aschers., non Bieb.)
A. sylvestris (L.) Hoffm.
*A. cerefolium (L.) Hoffm.

Seseli L.
S. libanotis (L.) Koch

Foeniculum Mill.
F. vulgare Mill.

Crithmum L.
C. maritimum L.

Oenanthe L.
O. fistulosa L.
O. pimpinelloides L.
O. silaifolia Bieb.
O. lachenalii C. C. Gmel.
O. crocata L.
O. aquatica (L.) Poir. (Phellandrium aquaticum L.)
O. fluviatilis (Bab.) Coleman

Aethusa L.
A. cynapium L.

Silaum Mill.
S. silaus (L.) Schinz & Thell. (Silaus flavescens Bernh., S. pratensis Bess.)

Meum Mill.
M. athamanticum Jacq.

Ligusticum L.
L. scoticum L.

Selinum L.
S. carvifolia (L.) L.

Angelica L. (incl. *Archangelica* Hoffm.)
A. sylvestris L.
*A. archangelica L. (Archangelica officinalis Hoffm.)

Peucedanum L.
P. officinale L.
P. palustre (L.) Moench
*P. ostruthium (L.) Koch

Pastinaca L.
P. sativa L. (Peucedanum sativum (L.) Hook. f.)

Heracleum L.
H. sphondylium L.
*H. mantegazzianum Somm. & Lev. (H. giganteum Host. non Fisch.)

Tordylium L.
*T. maximum L.

Coriandrum L.
*C. sativum L.

Daucus L.
D. carota L.
D. gingidium L. (D. gummifer auct., non All., D. maritimus With., non Lam.)

Caucalis L.
*C. latifolia L.
*C. daucoides L.

Torilis Adans.
T. arvensis (Huds.) Link (T. infesta (L.) Spreng.)
†T. anthriscus (L.) C. C. Gmel. (nom. illegit.; ? T. japonica (Houtt.) DC.)
T. nodosa (L.) Gaertn.

ARALIACEAE
Hedera L.
H. helix L.

CORNACEAE
Cornus L.
C. suecica L.
C. sanguinea L.

ADOXACEAE
Adoxa L.
A. moschatellina L.

CAPRIFOLIACEAE
Sambucus L.
S. nigra L.
*S. ebulus L.
*S. racemosa L.

Viburnum L.
V. opulus L.
V. lantana L.

Symphoricarpos Duham.
*S. albus (L.) S. F. Blake (S. racemosus Michx.)

Linnaea L.
L. borealis L.

Lonicera L.
*L. caprifolium L.
L. periclymenum L.
L. xylosteum L.

RUBIACEAE

Rubia L.

R. peregrina L.

Galium L.

G. boreale L.
G. cruciata (L.) Scop.
G. verum L.
G. erectum Huds.
G. mollugo L.
G. saxatile L. (G. hercynicum Weig.)
G. pumilum Murr. (G. sylvestre Poll., G. pusillum auct.)
G. palustre L.
  G. witheringii Sm.
G. debile Desv.
G. uliginosum L.
G. anglicum Huds.
*G. spurium L.
  *G. vaillantii DC.
G. aparine L.
G. tricorne Stokes

Asperula L.

A. odorata L.
*A. taurina L.
A. cynanchica L.
*A. arvensis L.

Sherardia L.

S. arvensis L.

VALERIANACEAE

Valeriana L.

V. dioica L.
V. officinalis L. (incl. V. sambucifolia Mikan)
*V. pyrenaica L.

Centranthus DC.

*C. ruber (L.) DC.

Valerianella Mill.

V. locusta L. (V. olitoria (L.) Poll.)
*V. eriocarpa Desv.
V. carinata Lois.
V. rimosa Bast. (V. auricula DC.)
V. dentata (L.) Poll.

DIPSACACEAE

Dipsacus L.

D. fullonum L. (D. sylvestris Huds.)
D. pilosus L.

Knautia L.

K. arvensis (L.) Coult.

Succisa Moench

S. pratensis Moench (Scabiosa succisa L.)

Scabiosa L.

S. columbaria L.
*S. atropurpurea L. (incl. S. maritima L.)

COMPOSITAE

Eupatorium L.

E. cannabinum L.

Solidago L.

S. virgaurea L.
  S. cambrica Huds.
  S. angustifolia Mill.

*S. lanceolata L.
*S. canadensis L.
*S. serotina Ait., ? non Retz.

Bellis L.

B. perennis L.

Aster L.

*A. salignus Willd.
*A. lamarckianus Nees (A. paniculatus Lam., non Mill.)
*A. longifolius Lam.
*A. novi-belgii L.
*A. macrophyllus L.
*A. laevis L.
A. tripolium L.
A. linosyris (L.) Bernh.

Erigeron L.

*E. canadensis L.
*E. mucronatus DC.
E. acris L.
E. borealis (Vierh.) Simmons (E. alpinus auct. angl.)
E. uniflorus L.

Filago L.

F. germanica (L.) L.
F. apiculata G. E. Sm.
F. spathulata J. & C. Presl
F. minima (Sm.) Pers.
*F. gallica L.

Antennaria Gaertn.

A. dioica (L.) Gaertn.
  A. hyperborea D. Don

Anaphalis DC.

*A. margaritacea (L.) Benth.

Gnaphalium L.

G. uliginosum L.
*G. undulatum L.
G. luteo-album L.
G. sylvaticum L.
G. norvegicum Gunn.
G. supinum L.

Inula L.

*I. helenium L.
I. conyza DC. (I. squarrosa (L.) Bernh., non L.)
I. salicina L.
*I. britannica L.
I. crithmoides L.
*I. viscosa (L.) Ait.

Pulicaria Gaertn.

P. dysenterica (L.) Bernh.
P. vulgaris Gaertn.

Ambrosia L.

*A. artemisiifolia L.

Xanthium L.

*X. spinosum L.

Rudbeckia L.

*R. laciniata L.

Bidens L.

B. cernua L.
B. tripartita L.

Galinsoga Ruiz & Pav.

  *G. parviflora Cav.
  *G. quadriradiata Ruiz & Pav.

Achillea L.

  A. millefolium L.
  A. ptarmica L.

Santolina L.

  *S. chamaecyparissus L.

Otanthus Hoffmgg. & Link

  O. maritimus (L.) Hoffmgg. & Link (Diotis maritima
    (L.) Sm.)

Anthemis L.

  *A. tinctoria L.
  A. cotula L.
  A. arvensis L.
  A. nobilis L.

Chrysanthemum L.

  C. segetum L.
  C. leucanthemum L.
  *C. parthenium (L.) Bernh.

Matricaria L.

  M. maritima L.
    M. inodora L.
  M. chamomilla L.
  *M. matricarioides (Less.) Porter (M. discoidea DC.,
    M. suaveolens (Pursh) Buchen., non L.)

Cotula L.

  *C. coronopifolia L.

Tanacetum L.

  T. vulgare L.

Artemisia L.

  A. absinthium L.
  A. vulgaris L.
  A. campestris L.
  A. maritima L.
  *A. stelleriana Bess.

Tussilago L.

  T. farfara L.

Petasites Mill.

  *P. fragrans (Vill.) C. Presl
  P. hybridus (L.) Gaertn., Mey. & Scherb. (P. ovatus
    Hill, P. officinalis Moench)
  *P. albus (L.) Gaertn.

Doronicum L.

  *D. pardalianches L.
  *D. plantagineum L.

Senecio L.

  S. vulgaris L.
  S. sylvaticus L.
  S. viscosus L.
  *S. squalidus L.
  S. erucifolius L.
  S. jacobaea L.
  S. aquaticus Hill
    S. erraticus Bertol.
  *S. sarracenicus L.
  S. paludosus L.
  S. congestus (R.Br.) DC. (S. palustris (L.) DC., non
    Vell.)

S. integrifolius (L.) Clairv. (S. campestris Retz. DC.)
  S. spathulifolius (C. C. Gmel.) Turcz.
  *S. doria L.
  *S. cineraria DC.

Carlina L.

  C. vulgaris L.

Arctium L.

  A. lappa L. (A. majus Bernh.)
  A. vulgare (Hill) A. H. Evans (incl. A. nemorosum
    Lej. & Court., A. pubens Bab. and A. inter-
    medium Lange)
  A. minus (Hill) Bernh.

Carduus L.

  *C. pycnocephalus L.
  C. tenuiflorus Curt.
  C. nutans L.
  C. crispus L.
    C. acanthoides L.

Cirsium Mill.

  C. vulgare (Savi) Ten. (C. lanceolatum (L.) Scop.,
    non Hill, Cnicus lanceolatus (L.) Willd.)
  C. eriophorum (L.) Scop. (Cnicus eriophorus (L.)
    Roth)
  C. palustre (L.) Scop. (Cnicus palustris (L.) Willd.)
  C. tuberosum (L.) All. (Cnicus tuberosus (L.) Roth)
  C. dissectum (L.) Hill (Cnicus pratensis (Huds.)
    Willd., Cirsium anglicum (Lam.) DC.)
  C. heterophyllum (L.) Hill (C. helenioides (L.) Hill,
    Cnicus heterophyllus (L.) Willd.)
  C. acaulos (L.) Scop. (Cnicus acaulos (L.) Willd.)
  C. arvense (L.) Scop. (Cnicus arvensis (L.) Hoffm.)
  *C. oleraceum (L.) Scop.

Cnicus L.

  *C. benedictus L.

Onopordum L.

  *O. acanthium L.

Silybum Adans.

  *S. marianum (L.) Gaertn.

Saussurea DC.

  S. alpina (L.) DC.

Serratula L.

  S. tinctoria L.

Centaurea L.

  *C. jacea L.
  C. nigra L. (C. obscura Jord.)
  C. nemoralis Jord.
  C. scabiosa L.
  *C. cyanus L.
  *C. paniculata L.
  C. aspera L.
  C. calcitrapa L.

Cichorium L.

  C. intybus L.
  *C. endivia L.

Arnoseris Gaertn.

  A. minima (L.) Schweigg. & Koerte

Lapsana L.

  L. communis L.

Picris L.
   P. hieracioides L.
   *P. spinulosa Guss.
   P. echioides L. (Helminthia echioides (L.) Gaertn.)

Crepis L.
   C. foetida L.
   *C. taraxacifolia Thuill.
   *C. setosa Haller
   C. capillaris (L.) Wallr. (C. virens L.)
   *C. nicaeensis Balb.
   C. biennis L.
   C. mollis (Jacq.) Aschers.
   C. paludosa (L.) Moench

Hieracium L.
   See list provided by Mr H. W. Pugsley on p. 345.

Hypochoeris L.
   H. glabra L.
   H. radicata L.
   H. maculata L.

Leontodon L.
   L. leysseri (Wallr.) Beck (L. taraxacoides (Vill.)
      Lacaita, non Mérat; Thrincia hirta auct.)
   L. hispidus L.
   L. autumnalis L.

Taraxacum Wigg.
   T. officinale Weber (T. vulgare Schrank)
   T. palustre (Lyons) DC.
   T. balticum Dahlst.
   T. spectabile Dahlst.
   T. laevigatum (Willd.) DC. (T. erythrospermum
      Bess.)
   T. obliquum (Fr.) Dahlst.

Lactuca L.
   L. virosa L.
   L. serriola L. (L. scariola L.)
   L. saligna L.
   L. muralis (L.) Fresen.
   L. alpina (L.) Hook. f.
   *L. macrophylla (Willd.) A. Gray

Sonchus L.
   S. oleraceus L.
   S. asper (L.) Hill
   S. arvensis L.
   S. palustris L.

Tragopogon L.
   T. pratensis L.
   T. minor Mill.
   *T. porrifolius L.

Scorzonera L.
   S. humilis L.

LOBELIACEAE
Lobelia L.
   L. dortmanna L.
   L. urens L.

CAMPANULACEAE
Jasione L.
   J. montana L.

Wahlenbergia Schrad.
   W. hederacea (L.) Rchb.

Phyteuma L.
   P. tenerum R. Schulz (P. orbiculare auct. angl.)
   P. spicatum L.

Campanula L.
   C. glomerata L.
   C. trachelium L.
   C. latifolia L.
   *C. rapunculoides L.
   C. rotundifolia L.
   *C. persicifolia L.
   *C. rapunculus L.
   C. patula L.
   *C. medium L.

Specularia P. C. Fabr.
   S. hybrida (L.) A.DC. (Legousia hybrida (L.) Delarb.)

VACCINIACEAE
Vaccinium L.
   V. vitis-idaea L.
   V. uliginosum L.
   V. myrtillus L.

Oxycoccus Hill
   O. quadripetalus Gilib. (Vaccinium oxycoccos L.)
   O. microcarpus Turcz.

ERICACEAE
Arbutus L.
   A. unedo L.

Arctostaphylos Adans.
   A. alpinus (L.) Spreng.
   A. uva-ursi (L.) Spreng.

Gaultheria L.
   *G. shallon Pursh

Andromeda L.
   A. polifolia L.

Calluna Salisb.
   C. vulgaris (L.) Hull

Erica L.
   E. ciliaris L.
   E. tetralix L.
   E. mackaiana Bab. (E. mackaii Hook.)
   E. cinerea L.
   E. vagans L.
   E. mediterranea L.

Loiseleuria Desv.
   L. procumbens (L.) Desv. (Azalea procumbens L.)

Ledum L.
   *L. palustre L.

Phyllodoce Salisb.
   P. caerulea (L.) Bab. (Bryanthus caeruleus (L.)
      Dippel)

Daboecia D. Don
   D. cantabrica (Huds.) C. Koch (D. polifolia D. Don)

Rhododendron L.
   *R. ponticum L.
   *R. luteum Sweet

PYROLACEAE

Pyrola L.
P. rotundifolia L.
P. media Sw.
P. minor L.
P. secunda L.

Moneses S. F. Gray
M. uniflora (L.) A. Gray

MONOTROPACEAE

Monotropa L.
M. hypopithys L.

PLUMBAGINACEAE

Limonium Mill.
L. vulgare Mill. (Statice limonium L.)
L. humile Mill. (Statice rariflora Drej., S. bahusiensis Fr.)
L. lychnidifolium (Gir.) O. Kuntze
L. binervosum (G. E. Sm.) C. E. Salmon
L. recurvum C. E. Salmon
L. transwallianum (Pugsl.) Pugsl.
L. paradoxum Pugsl.
L. bellidifolium (Gouan) Dum. (L. reticulatum auct. angl.)

Armeria Willd.
A. maritima Willd. (Statice armeria L.)
A. pubescens Link
A. plantaginea Willd.

PRIMULACEAE

Hottonia L.
H. palustris L.

Primula L.
P. vulgaris Huds.
P. veris L.
P. elatior (L.) Hill.
P. farinosa L.
P. scotica Hook.

Cyclamen L.
*C. hederifolium Ait. (C. europaeum auct., C. neapolitanum Ten.)

Lysimachia L.
L. thyrsiflora L.
L. vulgaris L.
*L. punctata L.
*L. ciliata L.
L. nummularia L.
L. nemorum L.

Trientalis L.
T. europaea L.

Glaux L.
G. maritima L.

Anagallis L.
A. arvensis L. (incl. A. phoenicea Scop.)
A. foemina Mill. (A. coerulea Schreb.)
A. tenella (L.) Murr.

Centunculus L.
C. minimus L.

Samolus L.
S. valerandi L.

OLEACEAE

Fraxinus L.
F. excelsior L.

Ligustrum L.
L. vulgare L.

LOGANIACEAE

Buddleja L.
*B. davidii Franch.

APOCYNACEAE

Vinca L.
*V. major L.
V. minor L.

GENTIANACEAE

Cicendia Adans.
C. filiformis (L.) Delarb. (Microcala filiformis (L.) Hoffmgg. & Link)

Blackstonia Huds.
B. perfoliata (L.) Huds. (Chlora perfoliata (L.) L.)

Centaurium Hill
C. umbellatum Gilib. (Erythraea centaurium (L.) Pers., non Borkh.)
C. latifolium (Sm.) Druce (Erythraea latifolia Sm.)
C. capitatum (Willd.) Borbás (Erythraea capitata Willd.)
C. littorale (D. Turner) Gilmour (Erythraea compressa Hayne, E. turneri Wheldon & Salmon)
C. pulchellum (Sw.) E. H. L. Krause (Erythraea pulchella (Sw.) Fr.)
C. tenuiflorum (Hoffmgg. & Link) Fritsch (Erythraea tenuiflora Hoffmgg. & Link)
C. portense (Brot.) Butcher (Erythraea portensis (Brot.) Hoffmgg. & Link)

Exaculum Caruel
E. pusillum (Lam.) Caruel (Cicendia pusilla (Lam.) Griseb.)

Gentiana L.
G. pneumonanthe L.
G. verna L.
G. nivalis L.
G. campestris agg.
G. campestris L. (G. germanica (Froel.) Murb., non Willd.)
G. baltica Murb.
G. amarella agg.
G. amarella L. (G. axillaris (Schmidt) Rchb.)
G. septentrionalis (Druce) Druce
G. anglica Pugsl. (G. lingulata Ag.)
G. uliginosa Willd.
G. germanica Willd.

MENYANTHACEAE

Menyanthes L.
M. trifoliata L.

Nymphoides Hill
N. peltatum (S. G. Gmel.) O. Kuntze (Limnanthemum peltatum S. G. Gmel.)

POLEMONIACEAE

Polemonium L.
P. caeruleum L.

BORAGINACEAE

Omphalodes Mill.
*O. verna Moench

Cynoglossum L.
C. officinale L.
C. germanicum Jacq. (C. montanum auct.)

Asperugo L.
*A. procumbens L.

Symphytum L.
S. officinale L.
S. tuberosum L.
*S. orientale L.
*S. peregrinum Ledeb.

Borago L.
*B. officinalis L.

Anchusa L.
*A. sempervirens L.

Lycopsis L.
L. arvensis L.

Pulmonaria L.
P. longifolia Bor. (P. angustifolia auct.)
*P. officinalis L.

Mertensia Roth
M. maritima (L.) S. F. Gray

Myosotis L.
M. sicula Guss.
M. caespitosa K. F. Schultz
M. scorpioides L. (M. palustris (L.) Hill)
M. secunda A. Murr. (M. repens Hook., non Donn)
M. brevifolia C. E. Salmon
M. alpestris Schmidt (M. pyrenaica auct.)
M. sylvatica (Ehrh.) Hoffm.
M. arvensis (L.) Hill
M. collina Hoffm.
M. versicolor Sm.

Lithospermum L.
L. purpurocaeruleum L.
L. officinale L.
L. arvense L.

Echium L.
E. vulgare L.
E. plantagineum L.

CONVOLVULACEAE

Calystegia R.Br.
C. sepium (L.) R.Br.
C. soldanella (L.) R.Br.
*C. sylvestris (Willd.) Roem & Schult. (C. inflata (Desf.) Don)

Convolvulus L.
C. arvensis L.

Cuscuta L.
C. europaea L.
C. epithymum (L.) Murr. (incl. C. trifolii Bab.)

SOLANACEAE

Solanum L.
S. dulcamara L.
S. nigrum L.

Lycium L.
*L. chinense Mill. (L. barbarum auct., p.p.)
*L. halimifolium Mill.

Atropa L.
A. bella-donna L.

Datura L.
*D. stramonium L.

Hyoscyamus L.
H. niger L.

SCROPHULARIACEAE

Verbascum L.
V. thapsus L.
*V. thapsiforme Schrad.
*V. phlomoides L.
V. pulverulentum Vill.
V. lychnitis L.
V. nigrum L.
*V. virgatum Stokes
*V. blattaria L.

Linaria Mill.
*L. cymbalaria (L.) Mill.
L. elatine (L.) Mill.
L. spuria (L.) Mill.
*L. supina (L.) Chazelles
*L. arenaria DC.
L. pelisseriana (L.) Mill.
*L. purpurea (L.) Mill.
L. repens (L.) Mill.
L. vulgaris Mill.
L. minor (L.) Desf.

Antirrhinum L.
*A. majus L.
A. orontium L.

Scrophularia L.
S. aquatica L.
S. umbrosa Dum. (S. alata Gilib.)
S. nodosa L.
S. scorodonia L.
*S. vernalis L.

Mimulus L.
*M. guttatus DC. (M. langsdorffii Donn, M. luteus auct. angl.)
*M. moschatus Lindl.

Limosella L.
L. aquatica L.
L. subulata Ives (L. tenuifolia Nutt.)

Sibthorpia L.
S. europaea L.

Digitalis L.
D. purpurea L.

Veronica L.
V. hederifolia L.
V. polita Fr. (V. didyma auct.)
V. agrestis L.

*V. persica Poir. (V. tournefortii C. C. Gmel. non
   Vill., V. buxbaumii Ten., non Schmidt)
*V. filiformis Sm.
V. triphyllos L.
V. verna L.
*V. praecox All.
*V. acinifolia L.
*V. peregrina L.
*†V. repens DC., non Gilib.: nom. illegit.
V. arvensis L.
V. serpyllifolia L.
V. humifusa Dicks. (V. borealis (Laest.) Hook. f.)
V. alpina L.
V. fruticans Jacq. (V. saxatilis Scop.)
V. spicata L.
V. hybrida L.
V. officinalis L.
V. chamaedrys L.
V. montana L.
V. scutellata L.
V. anagallis-aquatica L.
V. aquatica Bernh.
V. beccabunga L.

Euphrasia L.
   E. salisburgensis Funck
   E. officinalis agg.
      E. nemorosa (Pers.) Loehr
      E. confusa Pugsl.
      E. heslop-harrisoni Pugsl.
      E. occidentalis Wettst.
      E. pseudo-kerneri Pugsl. (E. kerneri auct., E.
         stricta auct.)
      E. cambrica Pugsl.
      E. curta (Fr.) Wettst.
      E. marshallii Pugsl.
      E. rotundifolia Pugsl.
      E. campbellae Pugsl.
      E. micrantha Rchb.
      E. frigida Pugsl. (E. latifolia auct., ? E. arctica
         Lange)
      E. eurycarpa Pugsl.
      E. foulaensis Towns.
      E. scotica Wettst.
      E. rhumica Pugsl.
      E. brevipila Burn. & Gremli
      E. borealis (Towns.) Wettst.
      E. hirtella Reut.
      E. anglica Pugsl.
      E. rivularis Pugsl.
      E. rostkoviana Hayne
      E. montana Jord.

Odontites Gilib.
   O. rubra Gilib. (Bartsia odontites (L.) Huds.)

Parentucellia Viv.
   P. viscosa (L.) Caruel (Bartsia viscosa L.)

Bartsia L.
   B. alpina L.

Pedicularis L.
   P. palustris L.
   P. sylvatica L.

Rhinanthus L.
   R. major agg.
      †R. major Ehrh.: nom illegit.
      R. aestivalis Zinger
      R. polycladus Chab.
      R. serotinus Schoenh. (R. montanus Saut.)
      R. borbasii Dörfl.

R. apterus (Fr.) Ostenf.
R. minor agg.
   R. minor L. (R. minor Ehrh.)
   R. stenophyllus (Schur) Druce
   R. calcareus Wilmott
   R. spadiceus Wilmott (R. monticola auct.)
   R. perrieri Chab. (R. rusticulus auct.)
   R. borealis (Sterneck) Druce (R. crista-galli var.
      drummond-hayi F. B. White)
   R. lintoni Wilmott
   R. lochabrensis Wilmott

Melampyrum L.
   M. cristatum L.
   *M. arvense L.
   M. pratense L.
   M. sylvaticum L.

OROBANCHACEAE

Orobanche L.
   O. ramosa L.
   O. purpurea Jacq. (O. arenaria auct.)
   O. rapum-genistae Thuill. (O. major auct. nonnull.)
   O. alba Steph. (O. rubra Sm.)
   O. caryophyllacea Sm.
   O. elatior Sutton (O. major auct. nonnull.)
   O. reticulata Wallr.
   O. apiculata Wallr. (? O. major L., O. minor Sm.,
      non Thunb.)
   O. picridis Hol.
   O. hederae Duby
   O. maritima Pugsl. (O. amethystea auct. angl.)

Lathraea L.
   L. squamaria L.
   *L. clandestina L.

LENTIBULARIACEAE

Utricularia L.
   U. vulgaris L.
   U. neglecta Lehm. (U. major auct.)
   U. minor L. (incl. U. bremii auct. angl., vix Heer)
   U. intermedia Hayne (incl. U. ochroleuca auct.
      angl., vix Hartm.)

Pinguicula L.
   P. vulgaris L.
   P. grandiflora Lam.
   P. alpina L.
   P. lusitanica L.

VERBENACEAE

Verbena L.
   V. officinalis L.

LABIATAE

Mentha L.
   M. rotundifolia (L.) Huds.
   *M. alopecuroides Hull ? of hybrid origin
   M. longifolia (L.) Huds.
   *M. spicata L. (M. viridis (L.) L.)
   M. piperita L. (incl. M. citrata Ehrh.) ? of hybrid
      origin
   M. aquatica L.
   M. verticillata L. ? of hybrid origin
   M. rubra Huds., non Mill. ? of hybrid origin
   M. gentilis L. ? of hybrid origin
   M. gracilis Sole ? of hybrid origin
   M. arvensis L.
   M. pulegium L.
   *M. requienii Benth.

Lycopus L.

L. europaeus L.

Origanum L.

O. vulgare L.

Thymus L.

T. serpyllum agg.
T. serpyllum L.
T. pycnotrichus (Uechtr.) Ronn.
T. lanuginosus Mill.
T. pseudo-lanuginosus Ronn.
T. drucei Ronn.
T. zetlandicus Ronn. & Druce
T. neglectus Ronn.
T. britannicus Ronn.
T. pulegioides agg.
T. pulegioides L. (T. ovatus Mill., T. chamaedrys Fr., p.p.)
T. glaber Mill. (T. chamaedrys Fr., p.p.)
T. carniolicus Déségl.

Clinopodium L.

C. vulgare L.

Acinos Mill.

A. arvensis (Lam.) Dandy, comb. nov. (Thymus acinos L., Calamintha arvensis Lam., C. acinos (L.) Clairv.)

Calamintha Mill.

C. baetica Boiss. & Reut.
C. nepeta (L.) Savi
C. ascendens Jord. (C. officinalis auct. angl.)
C. intermedia (Baumg.) H. Braun (C. sylvatica Bromf.)

Satureja L.

*S. montana L.

Hyssopus L.

*H. officinalis L.

Melissa L.

*M. officinalis L.

Salvia L.

S. horminoides Pourr. (S. verbenaca auct.)
S. verbenaca L. sec. Pugsl. (incl. S. marquandii Druce)
S. pratensis L.
*S. verticillata L.

Nepeta L.

N. cataria L.

Glecoma L.

G. hederacea L. (Nepeta glechoma Benth.)

Scutellaria L.

S. galericulata L.
S. minor Huds.

Prunella L.

P. vulgaris L.
*P. laciniata (L.) L.

Melittis L.

M. melissophyllum L.

Marrubium L.

M. vulgare L.

Stachys L.

S. officinalis (L.) Trev. (S. betonica Benth.)
S. germanica L.
S. palustris L.
S. sylvatica L.
S. alpina L.
S. arvensis (L.) L.
*S. annua (L.) L.

Galeopsis L.

*G. ladanum L. (G. intermedia Vill.)
G. angustifolia Hoffm. (G. ladanum auct. angl.)
G. dubia Leers (G. ochroleuca Lam.)
G. speciosa Mill. (G. versicolor Curt.)
G. tetrahit L.

Leonurus L.

*L. cardiaca L.

Lamium L.

L. amplexicaule L.
L. moluccellifolium Fr.
L. hybridum Vill.
L. purpureum L.
*L. maculatum L.
L. album L.

Galeobdolon Adans.

G. luteum Huds. (Lamium galeobdolon (L.) Crantz)

Ballota L.

B. nigra L.
*B. ruderalis Sw.

Teucrium L.

T. botrys L.
T. scordium L.
*T. chamaedrys L.
T. scorodonia L.

Ajuga L.

A. reptans L.
A. pyramidalis L.
*A. genevensis L.
A. chamaepitys (L.) Schreb.

PLANTAGINACEAE

Plantago L.

*P. psyllium L. (P. indica L., P. ramosa (Gilib.) Aschers.)
P. coronopus L.
P. sabrinae (Card. & Bak.) Druce
P. maritima L.
P. lanceolata L.
P. media L.
P. major L.

Littorella Berg.

L. uniflora (L.) Aschers. (L. lacustris L.)

ILLECEBRACEAE

Illecebrum L.

I. verticillatum L.

Herniaria L.

H. glabra L.
†H. ciliata Bab., non Clairv.: nom. illegit.

Corrigiola L.

C. littoralis L.

Scleranthus L.

S. annuus L.
S. perennis L.

AMARANTHACEAE

Amaranthus L.
  *A. retroflexus L.
  *A. albus L.

CHENOPODIACEAE

Chenopodium L.
  C. polyspermum L.
  C. vulvaria L. (C. olidum Curt.)
  C. album L.
  *C. reticulatum Aell.
  *C. viride L. sec. Aell. (C. suecicum J. Murr.)
  *C. opulifolium Schrad.
  C. ficifolium Sm. (C. serotinum auct.)
  C. murale L.
  C. hybridum L.
  C. urbicum L.
  C. rubrum L.
  C. botryodes Sm. (incl. C. crassifolium Hornem.)
  *C. glaucum L.
  *C. bonus-henricus L.
  *C. capitatum (L.) Aschers.

Beta L.
  B. maritima L.

Atriplex L.
  A. littoralis L.
  A. patula L.
  A. hastata L. (incl. A. deltoidea Bab.)
  A. glabriuscula Edmondst. (incl. A. babingtonii Woods)
  A. laciniata L. (A. maritima Hallier, A. sabulosa Rouy)

Obione Gaertn.
  O. portulacoides (L.) Moq. (Atriplex portulacoides L.)
  O. pedunculata (L.) Moq. (Atriplex pedunculata L.)

Salicornia L.
  S. perennis (Gouan) Mill. (S. radicans Sm.)
  S. lignosa Woods
  S. dolichostachya Moss
  S. stricta Dum. sec. Moss (S. europaea auct., S. herbacea auct.)
  S. ramosissima Woods
  S. pusilla Woods
  S. gracillima (Towns.) Moss
  S. appressa (Dum.) Dum.
  S. smithiana Moss (S. procumbens auct., non Sm.)
  S. prostrata Pall. sec. Moss
  S. disarticulata Moss

Suaeda Forsk.
  S. fruticosa Forsk.
  S. maritima (L.) Dum.

Salsola L.
  S. kali L.

POLYGONACEAE

Polygonum L.
  P. convolvulus L.
  P. dumetorum L.
  P. aviculare agg.
    P. aviculare L. (P. heterophyllum Lindm.)
    P. aequale Lindm.
    P. calcatum Lindm.
    P. rurivagum Bor.
    P. littorale Link

P. raii Bab.
P. maritimum L.
P. hydropiper L.
P. minus Huds.
P. mite Schrank (P. laxiflorum Weihe)
P. persicaria L.
P. lapathifolium L. (P. scabrum Moench)
P. nodosum Pers. (P. maculatum (S. F. Gray) Bab., P. petecticale (Stokes) Druce)
P. amphibium L.
P. bistorta L.
P. viviparum L.
*P. sagittatum L.
*P. polystachyum Meisn.
*P. cuspidatum Sieb. & Zucc.
*P. sachalinense Maxim.

Fagopyrum Moench
  *F. sagittatum Gilib. (Polygonum fagopyrum L.)

Oxyria Hill
  O. digyna (L.) Hill

Rumex L.
  R. conglomeratus Murr. (R. conglomeratus Schreb.)
  R. rupestris Le Gall
  *R. cuneifolius Campd.
  R. sanguineus L. (incl. R. condylodes Bieb. R. nemorosus Willd.))
  R. maritimus L.
  R. palustris Sm. (R. limosus auct. angl.
  *R. brownii Campd.
  *R. triangulivalvis (Danser) Rech. f.
  R. pulcher L.
  R. obtusifolius L.
  R. crispus L.
  *R. patientia L.
  R. domesticus Hartm. (R. longifolius auct. angl., ?DC., R. aquaticus Hook., non L.)
  R. hydrolapathum Huds.
  R. aquaticus L.
  *R. alpinus L.
  R. acetosa L.
  *R. scutatus L.
  R. acetosella L.

ARISTOLOCHIACEAE

Asarum L.
  A. europaeum L.

Aristolochia L.
  *A. clematitis L.

THYMELAEACEAE

Daphne L.
  D. mezereum L.
  D. laureola L.

ELAEAGNACEAE

Hippophae L.
  H. rhamnoides L.

LORANTHACEAE

Viscum L.
  V. album L.

SANTALACEAE

Thesium L.
  T. humifusum DC.

EUPHORBIACEAE

Euphorbia L.

  E. peplis L.
  E. helioscopia L.
  E. platyphyllos L.
  E. stricta L.
  E. hyberna L.
  *E. dulcis L.
  *E. corallioides L.
  *E. pilosa L.
  E. amygdaloides L.
  *E. esula L.
  *E. virgata Waldst. & Kit.
  E. cyparissias L.
  E. paralias L.
  E. portlandica L.
  E. peplus L.
  E. exigua L.
  *E. lathyrus L.

Mercurialis L.

  M. perennis L.
  *M. annua L.

BUXACEAE

Buxus L.

  B. sempervirens L.

ULMACEAE

Ulmus L.

  U. glabra Huds. (U. scabra Mill., U. montana Stokes)
  × U. hollandica Mill. (incl. U. vegeta (Loud.) Ley)
  U. carpinifolia Gleditsch (U. nitens Moench)
  U. diversifolia Melville (U. minor auct.)
  U. plotii Druce
  U. stricta Lindl.
  U. procera Salisb. (U. campestris auct. angl.)

CANNABINACEAE

Humulus L.

  H. lupulus L.

URTICACEAE

Urtica L.

  U. dioica L.
  U. urens L.

Parietaria L.

  P. diffusa Mert. & Koch (P. officinalis auct., P. ramiflora auct.)

MYRICACEAE

Myrica L.

  M. gale L.
  *M. caroliniensis Mill.

JUGLANDACEAE

Juglans L.

  *J. regia L.

BETULACEAE

Betula L.

  B. pendula Roth (B. verrucosa Ehrh., B. alba auct.)
  B. pubescens Ehrh.
  B. nana L.

Alnus Mill.

  A. glutinosa (L.) Gaertn. (A. rotundifolia Stokes)
  *A. incana (L.) Moench

CORYLACEAE

Carpinus L.

  C. betulus L.

Corylus L.

  C. avellana L.

FAGACEAE

Quercus L.

  Q. robur L.
  Q. petraea (Mattuschka) Liebl. (Q. sessiliflora Salisb.)
  *Q. cerris L.
  *Q. ilex L.

Castanea Mill.

  *C. sativa Mill. (C. vesca Gaertn.)

Fagus L.

  F. sylvatica L.

SALICACEAE

Salix L.

  S. pentandra L.
  S. triandra L.
  S. fragilis L.
  S. alba L.
  S. purpurea L.
  *S. daphnoides Vill.
  S. viminalis L.
  S. lapponum L.
  S. caprea L.
  S. aurita L.
  S. atrocinerea Brot. (S. cinerea auct. angl.)
  S. nigricans Sm. (S. andersoniana Sm.)
  S. phylicifolia L.
  S. arbuscula L.
  S. repens agg.
    S. repens L.
    S. arenaria L.
  S. lanata L.
  S. myrsinites L.
  S. herbacea L.
  S. reticulata L.

Populus L.

  *P. alba L.
  P. canescens (Ait.) Sm.
  P. tremula L.
  P. nigra L.
  *P. serotina Hart. (? P nigra × deltoides)

EMPETRACEAE

Empetrum L.

  E. nigrum L.
  E. hermaphroditum (Lange) Hagerup

CERATOPHYLLACEAE

Ceratophyllum L.

  C. demersum L.
  C. submersum L.

MONOCOTYLEDONES
HYDROCHARITACEAE

Elodea Michx.
  *E. canadensis Michx.

Hydrilla L. C. Rich.
  H. verticillata (L.f.) Royle

Hydrocharis L.
  H. morsus-ranae L.

Vallisneria L.
  *V. spiralis L.

Stratiotes L.
  S. aloides L.

ORCHIDACEAE

Hammarbya O. Kuntze
  H. paludosa (L.) O. Kuntze (Malaxis paludosa (L.) Sw.)

Liparis L. C. Rich.
  L. loeselii (L.) L. C. Rich.

Corallorhiza Chatel.
  C. trifida Chatel. (C. innata R.Br.)

Neottia L. C. Rich.
  N. nidus-avis (L.) L. C. Rich.

Listera R.Br.
  L. cordata (L.) R.Br.
  L. ovata (L.) R.Br.

Spiranthes L. C. Rich.
  S. spiralis (L.) Chevall. (S. autumnalis L. C. Rich.)
  S. aestivalis (Poir.) L. C. Rich.
  S. romanzoffiana Cham.
  S. gemmipara (Sm.) Lindl.

Goodyera R.Br.
  G. repens (L.) R.Br.

Epipogium R.Br.
  E. aphyllum Sw.

Cephalanthera L. C. Rich.
  C. rubra (L.) L. C. Rich.
  C. longifolia (L.) Fritsch (C. ensifolia L. C. Rich.)
  C. damasonium (Mill.) Druce (C. latifolia Janch., C. lonchophyllum (L.f.) Rchb. f. C. grandiflora S. F. Gray p.p., C. pallens L. C. Rich.)

Epipactis Sw.
  E. helleborine (L.) Crantz (E. latifolia (L.) All.)
  †E. purpurata Sm. (E. violacea Bor.)
  E. leptochila (Godf.) Godf.
  E. dunensis (T. & T. A. Steph.) Godf.
  †E. vectensis (T. & T. A. Steph.) Brooke & Rose
  E. pendula C. Thomas
  E. atropurpurea Raf. (E. atrorubens Schult.)
  E. palustris (L.) Crantz

Himantoglossum Spreng. emend. Koch
  H. hircinum (L.) Spreng. (Orchis hircina (L.) Crantz)

Anacamptis L. C. Rich.
  A. pyramidalis (L.) L. C. Rich. (Orchis pyramidalis L.)

Orchis L.
  O. ustulata L.
  O. purpurea Huds.
  O. militaris L.
  O. simia Lam.
  O. morio L.
  O. mascula (L.) L.
  O. laxiflora Lam.
  O. latifolia L. sec. Pugsl. (O. incarnata auct. angl.)
  O. praetermissa Druce
  O. purpurella T. & T. A. Steph.
  O. pardalina Pugsl. (O. latifolia auct. angl., p.p.)
  O. occidentalis (Pugsl.) Wilmott
  O. traunsteinerioides (Pugsl.) Pugsl.
  O. kerryensis Wilmott
  O. francis-drucei Wilmott
  O. ericetorum (E. F. Linton) E. S. Marshall (? O. elodes Griseb.)
  O. fuchsii Druce (? O. maculata L.)
  O. hebridensis Wilmott

Aceras R.Br.
  A. anthropophorum (L.) S. F. Gray

Ophrys L.
  O. apifera Huds. (incl. O. trollii Heg.)
  O. fuciflora (Crantz) Rchb. (O. arachnites Lam.)
  O. sphegodes Mill. (O. aranifera Huds.)
  O. insectifera L. (O. muscifera Huds.)

Herminium R.Br.
  H. monorchis (L.) R.Br.

Gymnadenia R.Br.
  G. conopsea (L.) R.Br.

Neotinea Rchb. f.
  N. intacta (Link) Rchb. f.

Leucorchis E. Meyer
  L. albida (L.) Schur (Habenaria albida (L.) R.Br.)

Coeloglossum Hartm.
  C. viride (L.) Hartm. (Habenaria viridis (L.) R.Br.)

Platanthera L. C. Rich.
  P. bifolia (L.) L. C. Rich. (Habenaria bifolia (L.) R.Br.)
  P. chlorantha (Cust.) Rchb. (Habenaria chlorantha (Cust.) Bab., non Spreng)

Cypripedium L.
  C. calceolus L.

IRIDACEAE

Iris L.
  I. foetidissima L.
  *I. spuria L.
  I. pseudacorus L.
  *I. germanica L.

Hermodactylus Mill.
  *H. tuberosus (L.) Mill.

Crocus L.
  *C. nudiflorus Sm.
  *C. albiflorus Schult. (C. vernus (L.) All., non Mill.)
  *C. biflorus Mill.

Romulea Maratti

 R. columnae Seb. & Maur.

Sisyrinchium L.

 S. bermudiana L. (S. angustifolium Mill.)
 *S. californicum (Ker-Gawler) Ait. f.

Gladiolus L.

 G. illyricus Koch

AMARYLLIDACEAE

Narcissus L.

 N. pseudo-narcissus L.
 *N. obvallaris Salisb.
 *N. hispanicus Gouan (N. major Curt.)
 *N. infundibulum Poir. (N. odorus auct. angl.)
 *N. biflorus Curt.
 *N majalis Curt. (N. poeticus auct.)

Galanthus L.

 G. nivalis L.

Leucojum L.

 L. aestivum L.
 *L. vernum L.

Sternbergia Waldst. & Kit.

 *S. lutea (L.) J. A. & J. H. Schult.

Allium L.

 *A. ampeloprasum L.
 A. babingtonii Borrer
 A. scorodoprasum L.
 A. sphaerocephalon L.
 A. vineale L.
 A. oleraceum L. (incl. A. carinatum Sm., non L.)
 *A. carinatum L.
 A. schoenoprasum L.
 A. sibiricum L.
 *A. triquetrum L.
 A. ursinum L.

DIOSCOREACEAE

Tamus L.

 T. communis L.

LILIACEAE

Ruscus L.

 R. aculeatus L.

Asparagus L.

 A. maritimus (L.) Mill.
 *A. officinalis L.

Polygonatum Mill.

 P. verticillatum (L.) All.
 P. multiflorum (L.) All.
 P. odoratum (Mill.) Druce (P. officinale All.)

Maianthemum Weber

 M. bifolium (L.) Schmidt

Convallaria L.

 C. majalis L.

Simethis Kunth

 S. planifolia (L.) Gren. & Godr. (S. bicolor (Desf.) Kunth)

Muscari Mill.

 M. racemosum (L.) Mill.

Scilla L.

 S. autumnalis L.
 S. verna Huds.
 S. non-scripta (L.) Hoffmgg. & Link (S. nutans Sm.)
 *S. hispanica Mill. (S. campanulata Ait.)

Ornithogalum L.

 *O. nutans L.
 O. umbellatum L.
 O. pyrenaicum L.

Lilium L.

 *L. martagon L.
 *L. pyrenaicum Gouan

Fritillaria L.

 F. meleagris L.

Tulipa L.

 *T. sylvestris L.

Gagea Salisb.

 G. lutea (L.) Ker-Gawler

Lloydia Salisb.

 L. serotina (L.) Rchb.

Colchicum L.

 C. autumnale L.

Narthecium (L.) Huds.

 N. ossifragum (L.) Huds.

Tofieldia Huds.

 T. pusilla (Michx.) Pers. (T. palustris auct., T. borealis (Wahlenb.) Wahlenb.)

Paris L.

 P. quadrifolia L.

JUNCACEAE

Juncus L.

 J. bufonius L.
 J. trifidus L.
 J. squarrosus L.
 J. compressus Jacq.
 J. gerardii Lois.
 *J. tenuis Willd. (J. macer S. F. Gray)
 *J. dudleyi Wiegand
 J. balticus Willd.
 J. filiformis L.
 J. inflexus L. (J. glaucus Sibth.)
 J. effusus L.
 J. conglomeratus L.
 J. maritimus Lam.
 J. acutus L.
 J. bulbosus L. (J. supinus Moench)
  J. kochii F. Schultz
 J. subnodulosus Schrank (J. obtusiflorus Hoffm.)
 J. mutabilis Lam. (J. pygmaeus L. C. Rich.)
 J. articulatus L. (J. lampocarpus Davies)
 J. alpinus Vill. (? J. alpino-articulatus Chaix)
  J. nodulosus Wahlenb.
  J. marshallii Pugsl.
 J. acutiflorus Hoffm. (J. sylvaticus Reichard, non Huds.)
 J. castaneus Sm.
 J. biglumis L.
 J. triglumis L.
 J. capitatus Weig.

Luzula DC.

L. forsteri (Sm.) DC.
L. pilosa (L.) Willd.
L. sylvatica (Huds.) Gaud. (L. maxima (Reichard) DC.)
L. arcuata (Wahlenb.) Wahlenb.
L. spicata (L.) DC.
L. campestris (L.) DC.
L. multiflora (Retz.) Lej.
*L. pallescens (Wahlenb.) Bess.
*L. luzuloides (Lam.) Dandy & Wilmott (L. nemorosa (Poll.) E. Meyer, non Baumg.)
*L. nivea (L.) DC.

TYPHACEAE

Typha L.
T. latifolia L.
T. angustifolia L.

SPARGANIACEAE

Sparganium L.
S. erectum L. (S. ramosum Huds.)
S. neglectum Beeby
S. simplex Huds.
S. angustifolium Michx. (S. affine Schnizl.)
S. minimum (Hartm.) Fr.

ARACEAE

Arum L.
A. maculatum L.
A. neglectum (Towns.) Ridley (A. italicum auct. angl.)

Acorus L.
*A. calamus L.

Calla L.
*C. palustris L.

LEMNACEAE

Lemna L.
L. trisulca L.
L. minor L.
L. gibba L.
L. polyrhiza L.

Wolffia Schleid.
W. arrhiza (L.) Wimm.

ALISMATACEAE

Alisma L.
A. plantago-aquatica L.
A. lanceolatum With.

Baldellia Parl.
B. ranunculoides (L.) Parl. (Alisma ranunculoides L., Echinodorus ranunculoides (L.) Engelm.)

Luronium Raf.
L. natans (L.) Raf. (Elisma natans (L.) Buchen.)

Sagittaria L.
S. sagittifolia L.
*S. rigida Pursh (S. heterophylla Pursh, non Schreb.)

Damasonium Mill.
D. alisma Mill. (D. stellatum Thuill.)

BUTOMACEAE

Butomus L.
B. umbellatus L.

JUNCAGINACEAE

Triglochin L.
T. palustris L.
T. maritima L.

SCHEUCHZERIACEAE

Scheuchzeria L.
S. palustris L.

POTAMOGETONACEAE

Potamogeton L.
P. natans L. (P. hibernicus (Hagstr.) Druce)
× P. fluitans Roth (P. crassifolius Fryer, P. sterilis Hagstr.: P. lucens × natans)
× P. sparganifolius Fr. (P. kirkii Syme, P. tiselii Richt.: P. gramineus × natans)
P. polygonifolius Pourr. (P. oblongus Viv., P. anglicus Hagstr.)
P. coloratus Hornem. (P. plantagineus Roem. & Schult.)
× P. billupsii Fryer (P. coloratus × gramineus)
× P. lanceolatus Sm. (P. perpygmaeus Druce: P. berchtoldii × coloratus)
P. nodosus Poir. (P. petiolatus Wolfg., P. drucei Fryer)
P. lucens L. (P. acuminatus Schumach., P. longifolius Poir.)
× P. zizii Roth (P. angustifolius auct. mult., P. coriaceus (Mert. & Koch) A. Benn., P. babingtonii A. Benn.: P. gramineus × lucens)
× P. decipiens Koch (P. upsaliensis Tisel., P. salignus Fryer, P. brotherstonii A. Benn., P. kupfferii A. Benn.: P. lucens × perfoliatus)
P. gramineus L. (P. heterophyllus Schreb., P. palustris Teesd., P. gracilis Wolfg., P. lonchites Tuckerm., P. varians Fryer, P. falcatus Fryer)
× P. nericius Hagstr. (P. alpinus × gramineus)
× P. nitens Weber (P. salicifolius Wolfg., P. lundii Richt., P. involutus (Fryer) H. & J. Groves: P. gramineus × perfoliatus)
P. alpinus Balb. (P. rufescens Schrad.)
× P. griffithii A. Benn. (P. macvicarii A. Benn.: P. alpinus × praelongus)
× P. prussicus Hagstr. (P. johannis Harrison: P. alpinus × perfoliatus)
× P. olivaceus G. Fisch. (P. venustus A. Benn.: P. alpinus × crispus)
P. praelongus Wulf.
× P. cognatus Aschers. & Graebn. (P. perfoliatus × praelongus)
× P. undulatus Wolfg. (P. crispus × praelongus)
P. perfoliatus L.
× P. cooperi (Fryer) Fryer (P. cymatodes Aschers. & Graebn., P. cymbifolius G. Fisch.: P. crispus × perfoliatus)
*P. epihydrus Raf. (P. nuttallii Cham. & Schlecht., P. pensylvanicus Cham. & Schlecht.)
P. friesii Rupr. (P. compressus auct. mult., P. mucronatus Sond.)
× P. lintonii Fryer (P. crispus × friesii)
P. rutilus Wolfg.
P. pusillus L. (P. panormitanus Biv.)
P. obtusifolius Mert. & Koch (P. gramineus auct. mult.)
P. sturrockii (A. Benn.) A. Benn. ? of hybrid origin

P. berchtoldii Fieb. (P. pusillus auct. mult., P. tenuissimus (Mert. & Koch) Rchb., P. lacustris (Pearsall & Pearsall f.) Druce, P. millardii Harrison)

P. trichoides Cham. & Schlecht.

× P. bennettii Fryer (P. crispus × trichoides)

P. compressus L. (P. zosteraefolius Schumach.)

P. acutifolius Link (P. cuspidatus Sm.)

P. crispus L. (P. serratus auct. mult.)

P. filiformis Pers.

× P. suecicus Richt. (P. filiformis × pectinatus)

P. pectinatus L. (P. marinus L., P. interruptus Kit., P. vaillantii Roem. & Schult., P. zosteraceus Fr., P. flabellatus Bab.)

P. densus L. (P. serratus L., P. setaceus L.)

RUPPIACEAE

Ruppia L.

R. spiralis Dum. (R. maritima auct. mult.)

R. maritima L. (R. rostellata Koch)

ZANNICHELLIACEAE

Zannichellia L.

Z. palustris L. (incl. Z. polycarpa Nolte)

Z. pedicellata Fr. (Z. maritima Nolte, incl. Z. pedunculata Rchb. and Z. gibberosa Rchb.)

APONOGETONACEAE

Aponogeton L.f.

*A. distachyos L.f.

ZOSTERACEAE

Zostera L.

Z. marina L.

Z. hornemanniana Tutin

Z. nana Roth

NAJADACEAE

Najas L.

N. flexilis (Willd.) Rostk. & Schmidt

N. marina L.

*N. graminea Del.

ERIOCAULACEAE

Eriocaulon L.

E. septangulare With.

CYPERACEAE

Cyperus L.

C. fuscus L.

C. longus L.

Eleocharis R.Br.

E. acicularis (L.) Roem. & Schult.

E. palustris (L.) Roem. & Schult.

E. uniglumis (Link) Schult.

E. multicaulis (Sm.) Sm.

E. parvula (Roem. & Schult.) B., N. & S. (Scirpus nanus Spreng., non Poir.)

Scirpus L.

S. pauciflorus Lightf.

S. caespitosus L. (Trichophorum austriacum Palla) S. germanicus (Palla) Christiansen

S. hudsonianus (Michx.) Fernald (Eriophorum alpinum L.)

S. fluitans L.

S. cernuus Vahl (S. filiformis Savi, S. pygmaeus (Vahl) A. Gray)

S. setaceus L.

S. holoschoenus L.

S. lacustris L.

S. tabernaemontani C. C. Gmel.

S. triqueter L.

S. americanus Pers. (S. pungens Vahl)

S. maritimus L.

S. sylvaticus L.

Blysmus Schult.

B. compressus (L.) Link (Scirpus compressus (L.) Pers., non Moench)

B. rufus (Huds.) Link (Scirpus rufus (Huds.) Schrad.)

Eriophorum L.

E. vaginatum L.

E. opacum (Björnstr.) Fernald

E. angustifolium Honck.

E. latifolium Hoppe

E. gracile Roth

Rhynchospora Vahl

R. fusca (L.) Ait. f.

R. alba (L.) Vahl

Schoenus L.

S. ferrugineus L.

S. nigricans L.

Cladium P.Br.

C. mariscus (L.) Pohl

Kobresia Willd.

K. simpliciuscula (Wahlenb.) Mackenzie (K. caricina Willd., K. bipartita Dalla Torre)

Carex L.

C. dioica L.

C. pulicaris L.

C. capitata L.

C. rupestris All.

C. pauciflora Lightf.

C. microglochin Wahlenb.

C. maritima Gunn. (C. incurva Lightf.)

C. divisa Huds.

C. chordorrhiza L.f.

C. disticha Huds. (C. intermedia Good.)

C. arenaria L.

C. diandra Schrank (C. teretiuscula Good.)

C. appropinquata Schumacher (C. paradoxa Willd., non Gmel.)

C. paniculata L.

C. vulpina L.

†C. otrubae Podp. (C. vulpina auct. occid.)

*C. vulpinoidea Michx.

C. spicata Huds. (C. contigua Hoppe, C. muricata auct. angl., p.p.)

C. pairaei F. Schultz (C. muricata auct. angl., p.p.)

C. polyphylla Kar. & Kir. (C. leersii F. Schultz. non Gmel.)

C. divulsa Stokes

C. echinata Murr. (C. stellulata Good.)

C. remota L.

C. elongata L.

C. leporina L. (C. tripartita All., C. bipartita All., C. lachenalii Schkuhr, C. lagopina Wahlenb.)

C. curta Good. (C. canescens auct., non L.)

C. ovalis Good. (C. leporina auct., non L.)

C. halleri Gunn. (C. norvegica Retz., C. vahlii Schkuhr, C. alpina Sw.)

C. atrata L.
C. canescens L. sec. Nelmes (C. fusca All., C. bux-
baumii Wahlenb., C. polygama Schkuhr)
C. bicolor All.
†C. elata All. (C. reticulosa Peterm., C. stricta Good.,
C. hudsonii A. Benn.)
C. acuta L. (C. gracilis Curt.)
C. bigelowii Torr. (C. rigida Good., ?C. concolor
R.Br.) C. hyperborea Drej.
C. aquatilis Wahlenb.
C. recta Boott (C. kattegatensis Fr.)
C. nigra (L.) Reichard (C. angustifolia Sm., C.
goodenovii Gay, C. vulgaris Fr., C. caespitosa
Good: incl. C. eboracensis Nelmes.)
C. juncella (Fr.) Fr.
C. flacca Schreb. (C. glauca Scop., C. diversicolor
auct., non Cr.)
C. paupercula Michx. (C. irrigua (Wahlenb.) Sm.,
C. magellanica auct., vix Lam.)
C. limosa L.
C. rariflora (Wahlenb.) Sm.
C. digitata L.
C. glacialis Mackenzie
C. ornithopoda Willd.
C. humilis Leyss.
C. montana L.
C. pilulifera L.
C. ericetorum Poll.
C. caryophyllea Latour. (C. verna Chaix, C. praecox
Jacq., non Schreb.)
C. filiformis L. sec. Nelmes (C. tomentosa auct.,
non L.)
C. pallescens L.
C. panicea L.
C. vaginata Tausch (C. sparsiflora (Wahlenb.)
Steud.)
C. atrofusca Schkuhr (C. ustulata Wahlenb.)
C. capillaris L.
C. pendula L.
C. strigosa Huds.
C. depauperata Good.
C. sylvatica Huds.
C. laevigata Sm. (C. helodes Link)
C. binervis Sm.
C. sadleri Linton
C. distans L.
C. punctata Gaud.
C. hostiana DC. (C. fulva Host, C. hornschuchiana
Hoppe)
C. extensa Good.
C. flava agg.
C. flava L.
C. lepidocarpa Tausch
C. tumidicarpa Anderss. (C. oederi subsp. oedocarpa
Anderss., C. flava var. minor Towns.)
C. serotina Mérat (C. oederi auct., non Retz.,
? C. viridula Michx.)
C. lasiocarpa Ehrh. (C. filiformis auct. angl., non L.)
C. hirta L.
C. pseudocyperus L.
C. acutiformis Ehrh. (C. paludosa Good.)
C. riparia Curt.
C. rostrata Stokes (C. ampullacea Good., C. inflata
auct., non Huds.)
C. vesicaria L.
C. grahami Boott
C. saxatilis L. (C. pulla Good.)

GRAMINEAE

Panicum L.
*P. mileaceum L.

Digitaria Haller
*D. ischaemum (Schreb.) Muhl.
*D. sanguinalis (L.) Scop. (Panicum sanguinale L.)

Echinochloa Beauv.
*E. crus-galli (L.) Beauv.

Setaria Beauv.
*S. viridis (L.) Beauv.
*†S. glauca (L.) Beauv.
*S. verticillata (L.) Beauv.

Spartina Schreb.
S. maritima (Curt.) Fernald (S. stricta (Ait.) Roth)
*S. alterniflora Lois.
S. townsendii H. & J. Groves

Leersia Sw.
L. oryzoides (L.) Sw.

Phalaris L.
*P. canariensis L.
*P. minor Retz.
P. arundinacea L.

Anthoxanthum L.
A. odoratum L.
*A. puelii Lec. & Lamotte

Hierochloë R.Br.
H. odorata (L.) Beauv.

Alopecurus L.
A. myosuroides Huds. (A. agrestis L.)
A. aequalis Sobol. (A. fulvus Sm.)
A. geniculatus L.
A. bulbosus Gouan
A. pratensis L.
× A. hybridus Wimm. (A. geniculatus × pratensis)
A. alpinus Sm.

Milium L.
M. effusum L.

Phleum L.
P. alpinum L.
P. pratense L.
P. nodosum L.
P. phleoides (L.) Karst. (P. boehmeri Wibel)
P. arenarium L.

Mibora Adans.
M. minima (L.) Desv.

Agrostis L.
A. setacea Curt.
A. canina L.
A. tenuis Sibth. (A. vulgaris With.)
A. gigantea Roth (A. nigra With.)
A. stolonifera L. (incl. A. alba auct.)
*A. semiverticillata (Forsk.) C. Christ. (A. verti-
cillata Vill.)

Polypogon Desf.
P. monspeliensis (L.) Desf.

× *Agropogon* P. Fourn.
× A. littoralis (Sm.) C. E. Hubbard (Polypogon littoralis
Sm.)

Calamagrostis Roth (non Adans.)
C. epigejos (L.) Roth
C. canescens (Web.) Gmel. (C. lanceolata Roth)
C. neglecta (Ehrh.) Gaertn., Mey. & Scherb.
C. scotica Druce (C. strigosa auct. angl., non Kunth)

Gastridium Beauv.
G. ventricosum (Gouan) Schinz & Thell. (G. lendigerum (L.) Gaud.)

Apera Adans.
A. spica-venti (L.) Beauv.
A. interrupta (L.) Beauv.

Ammophila Host
A. arenaria (L.) Link (Psamma arenaria (L.) Roem. & Schult.)

× *Ammocalamagrostis* P. Fourn.
× A. baltica (Fluegge) P. Fourn. (Ammophila baltica (Fluegge) Link)

Lagurus L.
L. ovatus L.

Aira L.
A. caryophyllea L.
A. praecox L.

Corynephorus Beauv.
C. canescens (L.) Beauv. (Weingaertneria canescens (L.) Bernh.)

Deschampsia Beauv.
D. caespitosa (L.) Beauv.
D. alpina (L.) Roem. & Schult.
D. setacea (Huds.) Hack.
D. flexuosa (L.) Trin.

Holcus L.
H. mollis L.
H. lanatus L.

Trisetum Pers.
T. flavescens (L.) Beauv.

Avena L.
*A. fatua L.
*A. strigosa Schreb.
*A. ludoviciana Durieu

Helictotrichon Besser
H. pubescens (Huds.) Pilger (Avena pubescens Huds.)
H. pratense (L.) Pilger (Avena pratensis L.)

Arrhenatherum Beauv.
A. elatius (L.) J. & C. Presl (A. avenaceum Beauv.)
A. tuberosum (Gilib.) Schultz

Cynodon Rich.
C. dactylon (L.) Pers.

Sieglingia Bernh.
S. decumbens (L.) Bernh. (Triodia decumbens (L.) Beauv.)

Phragmites Adans.
P. communis Trin. (Arundo phragmites L.)

Sesleria Scop.
S. caerulea (L.) Ard.

Cynosurus L.
*C. echinatus L.
C. cristatus L.

Koeleria Pers.
K. vallesiana (Honck.) Bertol.
K. gracilis Pers.
K. britannica (Domin) Druce
K. albescens DC.

Molinia Schrank
M. caerulea (L.) Moench

Catabrosa Beauv.
C. aquatica (L.) Beauv.

Melica L.
M. nutans L.
M. uniflora Retz.

Dactylis L.
D. glomerata L.

Briza L.
*B. maxima L.
B. media L.
B. minor L.

Poa L.
P. annua L.
P. infirma H.B.K. (P. exilis (Freyn) Murb.)
P. bulbosa L.
P. alpina L.
P. flexuosa Sm. (P. laxa auct.)
P. jemtlandica (Almq.) Richt.
P. glauca Vahl
P. nemoralis L.
P. balfouri Parn.
P. compressa L.
*P. chaixi Vill.
P. pratensis agg.
P. pratensis L.
P. subcaerulea Sm.
P. irrigata Lindm.
P. angustifolia L.
P. palustris L.
P. trivialis L.

Glyceria R.Br.
G. fluitans (L.) R.Br.
G. plicata Fr.
× G. pedicellata Towns. (G. fluitans × plicata)
G. declinata Bréb.
G. maxima (Hartm.) Holmb. (G. aquatica (L.) Wahlenb.)

Puccinellia Parl.
P. maritima (Huds.) Parl. (Glyceria maritima Huds. Mert. & Koch)
P. distans (L.) Parl. (G. distans (L.) Wahlenb.)
P. pseudo-distans (Crép.) Jans. & Wacht.
P. fasciculata (Torr.) Bickn. (G. borreri (Bab.) Ralfs)
P. rupestris (With.) Fern. & Weath. (G. procumbens Dum.)

Scleropoa Griseb.
S. rigida (L.) Griseb. (Festuca rigida (L.) Kunth)

Desmazeria Dum.
D. loliacea (Huds.) Nym. (Catapodium loliaceum (Huds.) Link, Festuca rottboellioides Kunth)

Vulpia Gmel.
- V. membranacea (L.) Dum. (Festuca uniglumis Sol.)
- V. ambigua (Le Gall) A. G. More (Festuca ambigua Le Gall)
- V. myuros (L.) Gmel. (Festuca myuros L.)
- V. bromoides (L.) S. F. Gray (Festuca sciuroides Roth)

Festuca L.
- F. ovina L. (incl. F. vivipara Sm.)
- F. tenuifolia Sibth. (F. capillata Lam.)
- F. longifolia Thuill. (F. duriuscula auct., non L., sec. Howarth)
- F. glauca Lam. (incl. F. caesia Sm.)
- *F. heterophylla Lam.
- F. rubra L. (incl. subspp. duriuscula Syme and fallax (Thuill.) Howarth)
- F. juncifolia St. Am.
- F. altissima All. (F. sylvatica (Poll.) Vill.)
- †F. pratensis Huds. (F. elatior L., p.p.)
- †F. arundinacea Schreb. (F. elatior L., p.p.)
- F. gigantea (L.) Vill.

× *Festulolium* Asch. & Graebn.

× F. loliaceum (Huds.) P. Fourn. (Festuca loliacea Huds.; Festuca pratensis × Lolium perenne)

Bromus L.
- B. ramosus Huds. (B. asper Murr.)
- B. erectus Huds.
- *B. inermis Leyss.
- B. madritensis L.
- B. rigidus Roth (B. maximus Desf.)
- B. gussonii Parl. (B. maximus auct. angl., p.p.)
- B. sterilis L.
- *B. tectorum L.
- *B. secalinus L.
- B. racemosus L.
- B. commutatus Schrad. (B. pratensis Ehrh.)
- †B. mollis L. sec. Holmbg. (B. hordeaceus auct.)
- †B. hordeaceus L. sec. Holmbg. (B. thominii Hard.)
- B. interruptus (Hack.) Druce
- B. lepidus Holmbg. (B. britannicus I. A. Williams)
- *B. laciniatus Beal

Brachypodium Beauv.
- B. sylvaticum (Huds.) Beauv.
- B. pinnatum (L.) Beauv.

Lolium L.
- L. perenne L.
- *L. multiflorum Lam. (L. italicum Braun)
- *L. temulentum L.

Agropyron Gaertn.
- A. caninum (L.) Beauv.
- A. donianum F. B. White
- A. repens (L.) Beauv.
- A. pungens (Pers.) Roem. & Schult.
- A. junceum (L.) Beauv.
- × A. laxum Fr. (A. acutum auct. angl.; A. junceum × pungens)

†*Lepturus* R.Br.
- †L. filiformis (Roth) Trin.
- †L. incurvus (L.) Druce

Nardus L.
- N. stricta L.

Hordeum L.
- †H. europaeum (L.) All. (H. sylvaticum Huds.)
- H. nodosum L. (H. pratense Huds.)
- H. murinum L.
- H. marinum Huds. (H. maritimum With.)

Elymus L.
- E. arenarius L.

CONIFERAE

CUPRESSACEAE

Juniperus L.
- J. communis L.
- J. sibirica Burgsd. (J. nana Willd.)

TAXACEAE

Taxus L.
- T. baccata L.

PINACEAE

Pinus L.
- P. sylvestris L.
- *P. pinaster Ait. (P. maritima Lam.)
- *P. nigricans Host (P. nigra Link, non Ait.)

Larix Mill.
- *L. decidua Mill. (L. europaea DC.)

Picea A. Dietr.
- *P. abies (L.) Karsten (P. excelsa (Lam.) Link)

Abies Mill.
- *A. alba Mill. (A. pectinata DC.)

Pseudotsuga Carr.
- *P. taxifolia (Poir.) Britt.

PTERIDOPHYTA

OPHIOGLOSSACEAE

Botrychium Sw.
- B. lunaria (L.) Sw.

Ophioglossum L.
- O. vulgatum L.
- O. lusitanicum L.

OSMUNDACEAE

Osmunda L.
- O. regalis L.

MARSILEACEAE

Pilularia L.
- P. globulifera L.

HYMENOPHYLLACEAE

Hymenophyllum Sm.
- H. tunbrigense (L.) Sm.
- H. peltatum (Poir.) Desv.

Trichomanes L.
- T. speciosum Willd. (T. radicans Sw.)

POLYPODIACEAE

Pteridium Scop.
   P. aquilinum (L.) Kuhn

Cryptogramma R.Br.
   C. crispa (L.) Hook. & Bauer (Allosorus crispus (L.) Bernh.)

Anogramma Link
   A. leptophylla (L.) Link (Gymnogramma leptophylla (L.) Desv.)

Adiantum L.
   A. capillus-veneris L.

Blechnum L.
   B. spicant (L.) Roth

Phyllitis Hill
   P. scolopendrium (L.) Newm. (Scolopendrium vulgare Sm.)

Asplenium L.
   A. marinum L.
   A. trichomanes L.
   A. viride Huds. (A. trichomanes-ramosum L.)
   A. obovatum Viv. (A. lanceolatum Huds.)
   A. adiantum-nigrum L.
   A. ruta-muraria L.
   A. septentrionale (L.) Hoffm.

Ceterach Garsault
   C. officinarum DC. (Asplenium ceterach L.)

Athyrium Roth
   A. filix-femina (L.) Roth
   A. alpestre (Hoppe) Rylands
   A. flexile (Newm.) Syme

Cystopteris Bernh.
   C. fragilis (L.) Bernh.
   C. regia Desv. (C. alpina Desv.)
   C. dickieana Sim
   C. montana (Lam.) Desv.

Woodsia R.Br.
   W. ilvensis (L.) R.Br.
   W. alpina (Bolton) S. F. Gray

Dryopteris Adans.
   D. filix-mas agg.
      D. filix-mas (L.) Schott (Lastrea filix-mas (L.) Presl)
      D. borreri Newm.
      D. abbreviata (DC.) Newm.
   D. villarsii (Bell.) Woynar (Lastrea rigida Presl)
   D. cristata (L.) A. Gray (Lastrea cristata (L.) Presl)
   D. dilatata (Hoffm.) A. Gray (Lastrea dilatata (Hoffm.) Presl)
   D. spinulosa (Müll.) Warr (Lastrea spinulosa (Müll.) Presl)
   D. aemula (Ait.) O. Kuntze (Lastrea aemula (Ait.) Brack.)

Polystichum Roth
   P. lonchitis (L.) Roth
   P. setiferum (Forsk.) Woynar (P. angulare (Kit.) Presl)
   P. aculeatum (L.) Roth (P. lobatum (Huds.) Woynar)

Thelypteris Schmidel
   T. palustris Schott (Dryopteris thelypteris (L.) A. Gray)
   T. oreopteris (Ehrh.) C. Chr. (Lastrea montana Moore)
   T. phegopteris (L.) Slosson (Phegopteris polypodioides Fée)

Gymnocarpium Newm.
   G. dryopteris (L.) Newm. (Dryopteris linnaeana C. Chr.)
   G. robertianum (Hoffm.) Newm. (Polypodium calcareum Sm.)

Polypodium L.
   P. vulgare L.

SALVINIACEAE

Azolla Lam.
   *A. filiculoides Lam.

EQUISETACEAE

Equisetum L.
   E. telmateia Ehrh. (E. maximum Lam.)
   E. arvense L.
   E. pratense Ehrh.
   E. sylvaticum L.
   E. palustre L.
   E. fluviatile L. (incl. E. limosum L.)
   E. hyemale L.
   E. moorei Newm.
   E. trachyodon Braun
   E. variegatum Weber & Mohr
   E. wilsoni Newm.

LYCOPODIACEAE

Lycopodium L.
   L. selago L.
   L. inundatum L.
   L. annotinum L.
   L. clavatum L.
   L. alpinum L.

SELAGINELLACEAE

Selaginella Beauv.
   S. selaginoides (L.) Link (S. spinulosa Braun)

ISOETACEAE

Isoetes L.
   I. lacustris L.
   I. echinospora Durieu
   I. hystrix Durieu

APPENDIX 1*

LIST OF BRITISH SPECIES OF *RUBUS*, AND KEY TO SECTIONS, SUBSECTIONS AND SERIES OF *EUBATUS*, SUPPLIED BY WM. WATSON

Rubus L.

NOTE. The first name in the line is the name adopted. Following it are given references to (i) a correct description, and wherever possible (ii) a figure of the plant (sometimes published under another name) in works likely to be the most easily accessible to British students. In a few instances a synonym in current use is added at the end of the line. Quoted names used in an incorrect application are printed in italics. An asterisk indicates that a figure will be found in the work quoted.

Where the valid name is followed by 'sp.nov.', 'comb.nov.' or 'nom.nov.' those terms should in use be replaced by 'W. Wats.'

In order not unduly to lengthen the list only widely distributed species are admitted, and the numerous dwarf genetic varieties are left out. It is not to be understood that omitted names are rejected.

Subgen. *CYLACTIS* (Rafin.) Focke
saxatilis Linn.; Hooker, p. 117; Syme, t. 441.

Subgen. *CHAMAEMORUS* Focke
Chamaemorus Linn.; Hooker, p. 116; Syme, t. 440.

Subgen. *IDAEOBATUS* Focke
idaeus Linn.; Rogers, p. 1; Syme, t. 442.

Subgen. *GLAUCOBATUS* Dumort.
caesius Linn.; ligerinus Genev. Monog. p. 19; Coste, t. 1180.
caesius Linn. var. arvalis Reich. Fl. G. exc. p. 608; Sud. t. ccvII. 8.

Subgen. *EUBATUS* Focke
Sect. I. SUBERECTI P. J. Muell.
nessensis W. Hall; suberectus Anders.; Rog. p. 21; Syme, t. 444; *Coste 1153.
scissus W. Wats.; *fissus* auctt.; Rog. p. 20; Sud. t. II; *Coste 1154.
plicatus W. & N.; Rog. p. 22; *Sud. p. 18; Fl. Dan. t. 2589.
Bertramii G. Braun ex Focke; biformis Boul. p. 40; *Coste 1156.
sulcatus Vest ex Tratt.; Rog. p. 21; *Coste 1158; *Sud. p. 17.
nitidus W. & N.; Rog. p. 22; *Coste 1157; Sud. t. v. 1–6.
fissus Lindl.; Rogersii Lint. Rog. p. 21; Sud. t. VIII.
integribasis P. J. Muell. in Boul., non Rog.; Boul. p. 42; *Sud. p. 20.
subintegribasis Druce; *integ.* Rog. p. 24, non P. J. Muell.
affinis W. & N.; Rog. p. 23; Boul. p. 43; *Sud. p. 21; *Coste 1159.
Briggsianus (Rog.) comb.nov.; affinis W. & N. var. Briggsianus Rog. p. 24.
nobilissimus (W. Wats.) comb.nov.; opacus Focke subsp. nobilissimus W. Wats. in J. B. 1933, p. 132; Sud. t. v, 9.
subopacus Sud. in Bouv.; op. f. minor Focke Rog. p. 23.

Sect. II. SPRENGELIANI Focke
Sprengelii Weihe; Rog. p. 46; Boul. p. 46; *Coste 1161; Fl. Dan. t. 1696, 1697.
hemistemon P. J. Muell. in Boul., non Rog.; Bab. Man.⁹ p. 115; Boul. p. 47; *Sud. p. 33.
Braeuckeri G. Braun.; Braeucker '292 Rubus-Arten', No. 38.
permundus nom.nov.; mundiflorus W. Wats. in Rep. BEC. 1937, p. 445, non Sud.
chlorothyrsos Focke; Focke Syn. p. 263; *Sud. p. 36.

Sect. III. SILVATICI P. J. Muell.
Subsect. (a) *Virescentes* Genev.
Series *Calvescentes* Genev. p.p.
castrensis W.-Dod. J. B. 1906, p. 63.
chaerophyllus Sag. & W. Schultze; Rep. BEC. 1928, p. 784; *Sud. p. 27.
Crespignyanus nom.nov.; *similatus* W. Wats. in Rep. BEC. 1937, p. 444, non P. J. Muell.

* *Editorial note.* Initial capitals for specific epithets have been retained in this Appendix at Mr Watson's request. Contributors to the Biological Flora are asked to note that they should use small initial letters throughout in their accounts.

lentiginosus Ed. Lees, Phyt. IV, p. 927; Bab. Man.⁹ p. 115.

polyoplus W. Wats.; perarmatus W. Wats. in Rep. BEC. 1930, p. 424; *Salteri* *Sud. p. 25, non Bab.

horridisepalus (Sud.) comb.nov.; chaerophyllus var. horridisepalus *Sud. p. 28.

chloophyllus *Sud. p. 45.

calvatus Ed. Lees ex Blox. in Kirby; Rog. p. 35; Bab. B. R. p. 133; *Sud. p. 55.

rhodanthus W. Wats. J. B. 1933, p. 224; *rhombifolius* in *Rep. BEC. 1928, p. 858.

monensis Bart. & Ridd; J. B. 1930, p. 184; 1933, p. 128; *latifolius* *Sud. p. 26. laetus W. Wats. nec E. F. Lint.

carpinifolius W. & N.; Rog. p. 26; Boul. p. 44; *Sud. p. 23; *Coste 1160.

mercicus Bagn.; Rog. p. 33; Rep. BEC. 1929, p. 170.

vulgaris W. & N. var. α viridis W. & N.; Rep. BEC. 1930, p. 423; *Sud. p. 23.

stanneus Bart. & Ridd. J. B. 1934, p. 231.

nitidoides W. Wats.; Rep. BEC. 1931, p. 765.

vulgaris W. & N. var. ε mollis W. & N.; Focke Syn. p. 142.

glanduliger W. Wats.; Rep. BEC. 1934, p. 794.

confertiflorus W. Wats.; J. B. 1935, p. 193; *holerythros* Rog. p. 25, non Focke.

gratus Focke; Rog. p. 36; Boul. p. 56; *Sud. p. 26; *Coste 1163.

Lindleianus Ed. Lees; Rog. p. 28; *Sud. p. 56; *Coste 1168.

Questierii L. & M.; Rog. p. 45; Boul. p. 47; *Sud. p. 39; *Coste 1164.

Bakeranus Bart. & Ridd.; J. B. 1935, p. 128.

nemoralis P. J. Muell.; Selmeri Lindeb.; *Rep. BEC. 1928, p. 858; *Sud. p. 24; Rog. p. 35.

oxyanchus *Sud. p. 38; *nemoralis* Rog. p. 30, non P. J. Muell.

cambrensis W. Wats.; nem. var. glabratus Rog. p. 31; Rep. BEC. 1929, p. 169.

Maassii Focke; *Sud. p. 37.

senticosus Koehl.; *Sud. p. 22; montanus Wirtg., Focke Syn. 127, cf. 414.

Series *Macrophylli* Bouv.

leucandrus Focke, Syn. p. 210; non Rog.; Sud. t. LIII, 6–8 (leucander).

danicus Focke ex F. & G.; Lange, Danske Fl.⁴ p. 780; *Sud. p. 29; purbeckensis Bart. & Ridd.

orbifolius Lef.; Boul. p. 51; *Sud. p. 50.

macrophyllus W. & N.; Rog. p. 43; Boul. p. 49; *Coste 1166; *Sud. p. 48.

piletostachys Gr. & Godr. Fl. Fr. 1, p. 548; Boul. p. 49.

chrysoxylon (Rog.) comb.nov.; mercicus subsp. chrysoxylon Rog. p. 34.

Salteri Bab.; B. R. p. 131, non Rog.

ramosus Blox. ex Briggs; Rog. p. 37.

subinermoides Druce ex Wats. *Rep. BEC. 1928, p. 859; macrophyllus Syme, t. 450; pubescens var. subinermis Rog. p. 41.

amplificatus Ed. Lees; Bab. B. R. p. 153, Man.⁹ p. 120.

Boulayi (Sud.) comb.nov.; macrophyllus var. Boulayi Sud. p. 48.

Series *Pyramidales* Bouv.

mollissimus Rog.; hirtifolius var. mollissimus (Rog.), p. 49; *Sud. p. 29.

eupectus (Sud.) comb.nov.; *Sud. p. 47; pyram. f. egl. Rog. p.p.

crudelis W. Wats.; J. B. 1933, p. 228.

Schlechtendalii var. anglicus Sud. p. 50.

hirtifolius P. J. Muell., non Rog.; London Nat. 1929, p. 70; Maass in A. & G. Fl. N-o. Deutsch. Flachl. p. 400.

pyramidalis Kalt.; Rog. p. 50; Boul. p. 53; *Sud. p. 46; *Coste 1167.

Series *Nemorenses* Sud.

silvaticus W. & N.; Rog. p. 41; Boul. p. 54; Fl. Dan. t. 2904; *Sud. p. 51; *Coste 1165.

durescens W. R. Lint.; Rog. p. 29.

egregius Focke; *Focke, R. E. p. 181; *Sud. p. 53.

Subsect. (b) *Discoloroides* Genev.

Series *Subvirescentes* Sud.

insularis Aresch.; Some Obs. p. 139; Lange, Danske Fl.⁴ p. 778; *discolor*, Fl. Dan. t. 2414.

iricus Rog. p. 49.

macroacanthos W. & N.; *R. G. p. 44; A. & G. Syn. VI, p. 506; *Sud. p. 58.

bröensis nom.nov.; umbraticus Lindeb. (non Muell.) Hb. Rub. Scand. 11; villic. f. silvestris F. & G. Bot. Tidsskr. Bd. 16, p. 69.

Gelertii K. Frid.; Rog. p. 56; *Sud. p. 55.

septentrionalis nom.nov.; confinis Lindeb. (non Muell.) Hb. Rub. Scand. 12; Aresch. Some Obs. p. 142.

atrocaulis P. J. Muell.; Pollichia, 1859, p. 163; Boul. p. 57.

incurvatus Bab.; B. R. p. 88; Rog. p. 27.

Favonii nom.nov.; *dumn.* var. transiens Sud., p. 47; Set. Br Rubi, no. 86 (Bere Wood).

villicaulis Koehl.; Wimmer, Fl. Schles.³ p. 628; Rog. p. 34; *Coste 1169.

Langei G. Jens. ex F. & G.; Lange, Danske Fl.⁴ p. 778.

Series *Subdiscolores* Sud.

cryptadenes Sud.; Rep. BEC. 1930, p. 429; *erythrinus* Briggs, J. B. 1890, p. 204.

rhombifolius Weihe; J. B. 1933, p. 225.

polyanthemos Lindeb.; *Sud. p. 61; *Rep. BEC. 1928, p. 857; pulcherrimus Neum. Rog. p. 32.

separinus Genev.; *Sud. p. 64; cissburiensis B. & R. J. B. 1931, p. 238.
prolongatus Boul. & Let.; Corbière Fl. Norm. p. 203; *Coste 1186; *Sud. p. 62; griseoviridis Bart. & Ridd.
acclivitatum nom.nov; argentatus var. clivicola A. Ley, J. B. 1896, p. 158; Rog. p. 40; argenteus var.
 clivic. Sud.; alt. var. gymnost. Sud.; clivicola (A. Ley) Druce, non clivicolus Sud.
herefordensis *Sud. p. 64; Rep. BEC. 1931, p. 763. pydarensis Rilstone.
consobrinus (Sud.) comb.nov; villicaulis subsp. consobrinus Sud. Rub. Pyr. 46; argenteus subsp. consobrinus
 *Sud. p. 58.
oplothyrsus *Sud. p. 60; *dumn.* *Sud., p. 47; curvispinis W. Wats.

Series *Imbricati* Sud.

imbricatus Hort; Rog. p. 26; Bab. B. R. p. 91; *Sud. p. 67.
londinensis (Rog.) W. Wats. in Rep. BEC. 1937, p. 442.
cardiophyllus L. & M.; Rog. p. 29; *Sud. p. 68; *Coste 1171; *Rep. BEC. 1928, p. 856.
Silurum (A. Ley) W. Wats.; nemoralis var. Silurum A. Ley, Rog. p. 31.
dumnoniensis Bab. J. B. 1890, p. 338; Rog. p. 32; non Sud.
rotundatus P. J. Muell. ex Genev.; *Sud. p. 41; *cariensis* Rog. p. 25; altiarcuatus Bart. & Ridd.
Lindebergii P. J. Muell.; Rog. p. 33; *Sud. p. 84.
errabundus nom.nov.; *Scheutzii* Rog., p. 31 excl. syn., non Lindeb.; *Sud. p. 38.

Sect. IV. Discolores P. J. Muell.
Subsect. (a) *Gypsocaulones* P. J. Muell.

ulmifolius Schott f.; *Coste 1174; *Rep. BEC. 1928, p. 858; rusticanus Rog. p. 40; Boul. p. 60.
Pseudo-bifrons (Sud.) Bouv.; propinquus var. Pseudo-bifrons Sud. p. 79; *discolor* Genev. Monog. p. 262.
propinquus P. J. Muell. in Pollichia 1859, p. 88; *Sud. p. 79.
Winteri P. J. Muell.; Focke Syn. p. 196; Boul. p. 70; *Sud. p. 78.

Subsect. (b) *Hedycarpi* Focke

bifrons Vest. ex Tratt.; Boul. p. 63; *Sud. p. 80; *Coste 1173; nem. var. cornub. R. & R.
vulnerificus Lef. ex Genev. em. Bouvet; Corbière Fl. Norm. p. 201; *Sud. p. 83.
cuspidifer M. & L.; Corb. l. c.; *Coste 1179; *Sud. p. 82.

Subsect (c) *Candicantes* Focke

neomalacus *Sud. p. 90; Bouvet, Rub. de l'Anjou, 2ᵐᵉ partie, p. 14.
falcatus Kalt. Fl. d. Aach. Beck. p. 266; Foerster, Fl. exc. Aachen, p. 94.
Brittonii Bart. & Ridd.; J. B. 1931, p. 191.

Sect. V. Vestiti Focke
Series *Virescentes* (Sud.), including series *Hebecaules* Sud. p.p., comb.nov.; type-species *lasiostachys* L. &. M.

flavescens M. & L.; *Sud. p. 118.
splendidus M. & L.; *Sud. p. 116.
polioclados W. Wats. Rep. BEC. 1928, p. 783.
curvidens A. Ley; Rog. p. 57.
lasiostachys L. & M.; hirtior W. Wats. Rep. BEC. 1931, p. 764; surrejanus Bart. & Ridd.
hebecaulis *Sud. p. 123.
hypomalacus Focke; *Sud. p. 30.
serratulifolius *Sud. p. 122.
Schmidelyanus *Sud. p. 119.
condensatus P. J. Muell.; *Sud. p. 124.
sciocharis (Sud.) comb.nov.; gratus subsp. sciocharis *Sud. p. 26; sciaphilus Lange, Fl. Dan. t. 3026;
 hirtifolius. Rog. p. 48.

Series *Hypoleuci* Sud.

eifeliensis Wirtg.; Foerster Fl. excurs. Aachen, p. 119; Schmidelyanus var. eifeliensis *Sud. p. 120.
macrostachys P. J. Muell.; *Sud. p. 105.
vestitus W. & N.; *leucostachys* Rog. p. 50 non Sm.; Boul. p. 88; *Coste 1187; *Sud. p. 101.
andegavensis Focke ex Bouv.; *Sud. p. 104.
leucostachys Sm.; Syme, t. 448; leucotrichus, Rep. BEC. 1927, p. 503.
acutidens Boul. & Gill.; *Sud. p. 104; Boul. p. 89.
adscitus Genev.; *Sud. p. 110; hypoleucus Boul. p. 85; *Coste 1188.
macrothyrsus Lange Fl. Dan. t. 2832, non Rog.; *Sud. p. 112.
conspersus W. Wats. J. B. 1935, p. 255.
Boraeanus Genev.; Boul. p. 87; *Sud. p. 110.
criniger (E. F. Lint.) Rog.; Rog. p. 52.
Wolley-Dodii (Sud.) comb.nov.; macrostachys microgene Wolley-Dodii *Sud. p. 106; Set. Br. Rubi, no. 89,
 Edge Park.
adenanthus Boul. & Gill.; Rog. p. 53.
cordifolius W. & N.; *Sud. p. 45.
orbus nom.nov.; iricus var. minor R. & R. J. B. 1910, p. 318.
podophyllus P. J. Muell.; *Sud. p. 108; Focke in A. & G. Syn. d. mitteleurop. Fl. vi, p. 586; cinerosiformis
 Rilstone.
conspicuus P. J. Muell.; *Sud. p. 104; Focke Syn. 296.

Sect. nova VI. Rotundifolii

rotundifolius (Bab.) Blox. in Kirby; Drejeri, Rog. p. 62; Fl. Dan. t. 3023; *Sud. p. 151.
hibernicus (Rog.) comb.nov.; Drejeri G. Jensen subsp. hibernicus Rog. p. 62.
dunensis Rog.; Drejeri G. Jensen var. dunensis Rog.; J. B. 1901, p. 382.
Leyanus Rog.; Drejeri G. Jensen subsp. Leyanus Rog. p. 62.
Lettii Rog. J. B. 1901, p. 381.
mucronifer *Sud. p. 112; mucronatus Rog. p. 55.
mucronatiformis (Sud.) comb.nov.; hypomalacus subsp. mucronatiformis *Sud. p. 30; mucronatus Blox. var. nudicaulis Rog. p. 56.
cinerosus Rog. p. 54; apiculatus Weihe var. cinerosus *Sud. p. 133.
mucronatoides A. Ley J. B. 1907, p. 446; Rog. p. 55.
bracteosus Weihe; *Sud. p. 30; orthoclados Rog. p. 47.
fuscicortex *Sud. p. 114; *podophyllus* Rog. p. 67, non P. J. Muell.

Sect. VII. Radulae Focke

Series *Micantes* Sud.

Radula Weihe; Rog. p. 63; Boul. p. 89; *Coste 1184; *Sud. p. 127.
aspericaulis L. & M.; Boul. p. 90; *Sud. p. 129.
sectiramus W. Wats. London Nat. 1932, p. 60.
discerptus P. J. Muell.; *Coste 1191; *Sud. p. 132; *Rep. BEC. 1928, p. 861; echinatus Rog. p. 64.
echinatoides (Rog.) Druce; radula subsp. echinatoides Rog. p. 64; *Sud. p. 129; *Rep. BEC. 1928, p. 860.
Genevierii Bor.; Boul. p. 91; *Sud. p. 131; *Coste 1190.
cenomanensis *Sud. p. 113.
rudis Weihe; Rog. p. 65; Boul. p. 98; *Coste 1194; *Sud. p. 166.
pulcher M. & L.; Boul. p. 90; *Sud. p. 136; *festivus* Rep. BEC. 1929, p. 168.
radulicaulis Sud.; *sertiflorus* Rog. p. 64; *Radula* Syme, t. 452.

Series *Concolores* Sud.

regillus A. Ley; Rog. p. 67.
micans Gren. & Godr. Fl. Fce. i, p. 546 (non Rog.); *Sud. p. 134; *Coste 1183.
granulatus M & L.; *Sud. p. 139; oigocladus var. Bloxamianus Rog. p. 66.
rhenanus P. J. Muell.; *thyrsiflorus* Wirtg. Fl. d. preussisch. Rheinpr. pp. 148, 158., non Weihe & Nees.
prionodontus L. & M.; Boul. p. 94; *Sud. p. 143; radula var. cantianus W. Wats. in Rep. BEC. 1931, p. 767.

Sect. VIII. Apiculati Focke

Series nova *Foliosi*

foliosus Weihe; Focke Syn. p. 330; *Sud. p. 145.
flexuosus M. & L.; *Sud. p. 146; saltuum, *Rep. BEC. 1928, p. 862; *foliosus* Rog. p. 78; *Coste 1206.
corymbosus P. J. Muell.; Boul. p. 95; *Sud. p. 145.
homalodontus P. J. Muell & Wirtg.; *Sud. p. 147.
cavatifolius P. J. Muell.; Rog. p. 71; *Sud. p. 147.
acutipetalus L. & M.; Boul. p. 95; *Sud. p. 143.
drymophilus M. & L.; *Sud. p. 154.
fuscus Weihe, non Rog.; Focke Syn. p. 339; *Sud. p. 142; *Coste 1189.
rubristylus W. Wats. Rep. BEC. 1936, p. 220; *Newbouldii* Rog. p. 66., non. Bab.
sagittarius Ridd.; mutabilis subsp. nemorosus, Rog. p. 72.
Bloxamii Ed. Lees; Rog. p. 72; Bab. B. R. p. 169; *Sud. p. 154.
Menkei Weihe; Weihe & Nees R. G. p. 66; *Coste 1197.
chlorocaulon (Sud.) comb.nov.; pallidus subsp. chlorocaulon *Sud. p. 154.
Adamsii Sud.; fuscus var. Adamsii Sud.; Babingtonii var. phyllothyrsus (Frider.) Rog. p. 70.

Series nova *Pallidi*

pallidus Weihe; Rog. p. 74; Boul. p. 93; *Sud. p. 153.
euryanthemus nom.nov.; pallidus var. leptopetalus Frid. ex Rog. p. 75.
Loehri Wirtg. Fl. Rheinpr. p. 162; Focke Syn. p. 328; Sud. t. CLI, 1–4.
insectifolius L. & M. Pollichia 1859, p. 176; Boul. p. 95; f. var. nutans Rog. p. 74; nuticeps Bart. & Ridd.
foliolatus M. &. L. Pollichia 1859, p. 212; Sud. p. 155.
largificus W. Wats. Rep. BEC. 1931, p. 766.
acutifrons A. Ley; Rog. p. 90.
laxatifrons nom.nov.; acutifrons var. amplifrons A. Ley, J. B. 1902, p. 69, non R. amplifrons Sud.
glareosus Marsh. ex Rog. J. B. 1912, p. 309; *Rep. BEC. 1928, p. 861.
Rilstonei Bart. & Ridd., Proc. Cotteswold Club, XXIV, p. 213.
brachyadenes P. J. Muell.; *Sud. p. 161.
acidophyllus Sud. (nom.emend.); aciophyllus Sud. Diagn. p. 40; aciphyllus *Sud. p. 156.
fusciformis Sud. p. 154.
Lintoni Focke ex Bab.; Rog. p. 76; *Sud. p. 140.
cyclophorus (Sud.) comb.nov.; melanoxylon microgene cyclophorus *Sud. p. 165.
morganwgensis Bart. & Ridd. Proc. Cotteswold Club, XXIV, p. 218.

Series nova *Scabri*

  scaber Weihe; *Sud. p. 193; *Coste 1201.

  microdontus M. & L.; J. B. 1935, p. 197; conspectus Genev. p.p.

  curtiglandulosus (Sud.) comb.nov.; tereticaulis subsp. curtiglandulosus *Sud. p. 196.

  derasus L. & M.; *Sud. p. 146.

  vallisparsus *Sud. p. 168.

  praetextus *Sud. p. 171.

  thyrsiflorus Weihe; *Sud. p. 152; J. B. 1937, p. 201.

  longithyrsiger Ed. Lees ex Bab. B. R. p. 231; Rog. p. 77; *Sud. p. 146.

  botryeros (Focke ex Rog.) Focke; longithyrsiger var. or subsp. botryeros Focke ex Rog., Rog. p. 77.

Series nova *Obscuri*

  obscurus Kalt.; *Sud. p. 156; Foerster, Fl. excurs. Aachen, p. 122.

  cruentatus P. J. Muell. Pollichia, 1859, p. 294; Foerster, Fl. excurs. Aachen, p. 121.

  erraticus *Sud. p. 158.

  entomodontos P. J. Muell.; *Sud. p. 157.

  obscurissimus *Sud. p. 159.

  Purchasianus (Rog.) Druce; Rog. p. 80.

  insericatus P. J. Muell.; *Sud. p. 148.

  hyposericeus *Sud. p. 150; f. var. macrostachys Rog. p. 74 ; fuscoviridis Rilstone.

  rhombophyllus M. & L. Pollichia, 1859, p. 175; *Sud. p. 148.

  Gravetii (Boul. ex Sud.) comb.nov.; insericatus subsp. Gravetii Boul. ex Sud., *Sud. p. 149

  adornatiformis (Sud.) Bouv.; *Sud. p. 150; rosaceus, Genev. Monog. p. 140.

  scabripes Genev. Monog. p. 94; Sud. p. 179.

  rufescens L. & M.; *Sud. p. 181; *Rep. BEC. 1928, p. 863; rosaceus subsp. infecundus Rog. p. 80; *rosaceus* Bab. Man.[9] p. 122.

Series nova *Incompositi*

  sertiflorus P. J. Muell. ex Genev. monente Boul. (non Rog.); Sud. p. 131; Genev. Monog. p. 164.

  spurius Neum.; infestus auctt. non W. & N.; Rog. p. 59.

  ahenifolius nom.nov.; *dentatifolius* W. Wats. London Nat. 1930, p. 73, non Briggs.

  apiculatus Weihe; *Sud. p. 132; anglosax. Rog. p. 57.

  euanthinus nom.nov.; anglosaxonicus subsp. vestitiformis A. Ley ex Rog., Rog. p. 58.

  raduloides (Rog.) Druce; anglosaxonicus subsp. raduloides Rog., Rog. p. 58.

  heterobelus *Sud. p. 139; *praeruptorum* Rog. J. B. 1892, p. 301.

  tardus W. Wats. Rep. BEC. 1934, p. 794.

  Griffithianus Rog. in Griff.; Rog. p. 68; *Sud. p. 132.

  melanoxylon Muell. & Wirtg., non Rog.; *Sud. p. 164.

  melanodermis Focke; Rog. p. 69; tumulorum Rilstone.

  dentatifolius (Briggs) W. Wats.; Borreri var. dentatifolius Briggs, Rog. p. 61.

  vectensis W. Wats. in J. B. 1937, p. 197; *Borreri* Rog. p. 61; *Sud. p. 120.

  pascuorum nom.nov.; Borreri var. virgultorum Rog. p. 60.

  phaeocarpus W. Wats. J. B. 1937, p. 157; *Babingtonii*, Rog. p. 69; *Sud. p. 151.

Sect. IX. GRANDIFOLII Focke

Lejeunei Weihe; *Sud. p. 177.

Moylei Bart. & Ridd.; Lej. var. ericet. Rog. p. 71.

Turneri W. Wats. J. B. 1937, p. 158.

furvicolor Focke, R. E. p. 440; *melanox.* Rog. p. 59.

hostilis Muell. & Wirtg.; *Sud. p. 174; Foerster Fl. excurs. Aachen, p. 134; London Nat. 1934, p. 60.

festivus Muell. & Wirtg.; Focke Syn. p. 314.

diversus W. Wats. Rep. BEC. 1927, p. 508; *Kalt.* Rog. p. 88.

Leightoni Ed. Lees ex Leight. Fl. Shropsh. p. 233; anglic. Rog. p. 63; ericet. *Sud. p. 128.

breconensis nom.nov.; *Lejeunei* Rog. p. 70.

hastiformis nom.nov.; thyrsiger Bab., non Banning & Focke; Rog. p. 76.

rosaceus Weihe, non auctt.; *Rep. BEC. 1928, p. 862; London Nat. 1932, p. 64.

Powellii Rog. p. 81.

formidabilis L. & M.; *Sud. p. 178; Andersonii Rep. BEC. 1927, p. 499.

mutabilis Genev., non Rog.; *Sud. p. 176.

Naldretti (J. W. White) comb.nov., Rep. Wats. BEC. 1907, p. 86; *Koehleri* Syme, t. 453.

Wedgwoodiae Bart. & Ridd. Proc. Cotteswold Club, XXIV, p. 212; mut. var. Regnorum W. Wats. Rep. BEC. 1930, p. 437.

angusticuspis Sud.; anglosaxonicus subsp. setulosus Rog. p. 58.

Hiernii Ridd. Fl. Devon. p. 281; hirtus var. rotundifolius Rog. p. 88.

Sect. X. HYSTRICES Focke

Hystrix Weihe; W. & N. *R. G. p. 92; Focke Syn. p. 347; *Sud. p. 180.

hylocharis nom.nov.; rosaceus var. silvestris Murray ex Rog. in J. B. 1894, p. 47; Murray, Fl. Som. p. 116, 1896; Set Brit. Rubi no. 99 (Porlock).

hypochlorus *Sud. p. 176; Bouv. l. c. III[me] partie, p. 17.

semiglaber (Rog.) comb.nov.; Marshalli var. semiglaber Rog.; Rog. p. 84.

Marshalli Focke & Rog.; Rog. p. 84.
fusco-ater Weihe; Rog. p. 82; *Sud. p. 172.
absconditus L. & M.; *Sud. p. 173.
adornatus Muell. in Wirtg.; Boul. p. 102 non Rog.; *Sud. p. 173.
dasyphyllus Rog. p. 83; *Rep. BEC. 1928, p. 863.
humifusus Weihe; W. & N. *R. G. p. 84; *Sud. p. 204.
infestus Weihe non auctt.; W. & N. *R. G. p. 77; London Nat. 1930, p. 71.
newbridgensis Bart. & Ridd.; J. B. 1936, p. 204.
spinulifer M. & L.; Boul. p. 105; *Sud. p. 185.
ochrodermis A. Ley; Rog. p. 91.
pygmaeus Weihe; *Sud. p. 187.
pygmaeopsis Focke Syn. p. 364; Sud. p. 186; Foerst. l. c. p. 141.
apricus var. sparsipilus W. Wats. London Nat. 1934, p. 62; *apricus* Rep. BEC. 1927, p. 502.
Murrayi Sud.; *adornatus* Rog. p. 80.
spinulatus Boul.; *Sud. p. 185; *setiger* London Nat. 1930, p. 70.
Hartmani Gand. ex Sud. in Gand.; fusco-ater subsp. Hartmani (Gand.) *Sud. p. 173; horridus Hartm. Handb.[11] p. 282; Fl. Dan. Suppl. t. 77; Aresch. l. c. p. 118.
pilocarpus Gremli Beitr. Fl. Schw. p. 42; Fl. Switz. p. 135; obtruncatus subsp. pilocarpus (Gremli) *Sud. p. 177.
adenolobus W. Wats. London Nat. for 1934, p. 61; R. Koehl. var. cogn. (N. E. Brown) Rog. p. 83.

Sect. XI. GLANDULOSI P. J. Muell.

Series nova *Feroces*

Schleicheri Weihe; *Sud. p. 198; *Coste 1200.
dissectifolius *Sud. p. 200.
viridis Kalt. Fl. Aachen, p. 284; Foerst. l. c. p. 144.
aristisepalus (Sud.) comb.nov.; *velatus* Rog. p. 92, non Lef.

Series nova *Imbelles*

Durotrigum R. P. Murr. J. B. 1892, p. 15; Rog. p. 85.
angustifrons Sud.; serpens subsp. angustifrons *Sud. p. 217.
vepallidus (Sud.) comb.nov.; serpens subsp. vepallidus *Sud. p. 217.
hylonomus L. & M.; serpens microg. hylonomus (L. & M.) *Sud. p. 219.
leptadenes Sud. in Gand.; serpens subsp. leptadenes (Sud. in Gand.) *Sud. p. 219.
hirtus W. & K.; *Sud. p. 221; Boul. p. 121; Focke Syn. p. 371; *Coste 1205.
pallidisetus Sud.; *divexiramus* Rog. p. 86.
perplexus P. J. Muell. in Wirtg.; Kaltenbachii Focke Syn. 375, non Rog.; Foerst. l. c. p. 148; hirtus subsp. Kaltenbachii (Metsch) *Sud. p. 228.
Bellardii Weihe; Rog. p. 86; *Sud. p. 206; Fl. Dan. t. 1696; *Coste 1204. Syme, t. 454 *glandulosus*.

Sect. XII. CORYLIFOLII Focke

Series *Sub-Silvatici* Focke

latifolius Bab. B. R. p. 94; Man.[9] p. 117; J. B. 1930, p. 184 (non Rog.).
Balfourianus Blox. ex Bab.; Bab. B. R. p. 255; Man.[9] p. 128; Rog. p. 96; *Sud. p. 237.
umbelliformis M. & L.; Sud. p. 238.
semipyramidalis *Sud. p. 237.
Warrenii Sud.; dumet. var. concinnus Rog. p. 95.

Series *Sub-Discolores* Focke

sublustris Ed. Lees; Rog. p. 96; Bab. Man.[9] p. 129; Syme, t. 455.
conjungens (Bab.) W. Wats.; Bab. B. R. p. 265; Man.[9] p. 129; Rog. p. 96; *Rep. BEC. 1928, p. 865.
Wahlbergii Arrhen.; *Sud. p. 239.

Series nova *Sub-Radulae*

raduliformis (A. Ley) W.Wats.; J. B. 1904, p. 120.
cuspidatus P. J. Muell.; *Sud. p. 247.
adenoleucus Chab. Et. specif. du g. Rubus p. 358; Sud. t. ccxi, figs. 1, 2.
Babingtonianus nom.nov.; althaeif. Bab. non Host B. R. p. 274; Man.[9] p. 129.

Series *Sub-Glandulosi* Focke

tuberculatus Bab. B. R. p. 280; Rog. p. 94; J. B. 1870, t. 106.
rubriflorus Purch.; Rog. p. 94.
tenuiarmatus Ed. Lees in Phyt. iv, p. 818; dumet. var. triangularis A. Ley in J. B. 1902, p. 70.
myriacanthus Focke; diversifolius Rog. p. 93; J. B. 1870, t. 107.
scabrosus P. J. Muell.; dumet. var. ferox Rog. p. 93.
britannicus Rog. p. 93.

AUTHORS QUOTED

A. & G.	P. Ascherson and P. Graebner, *Synopsis der Mitteleuropäischen Flora*, Band VI (1).
Bab. B. R.	C. C. Babington, *The British Rubi*.
Bab. Man.⁹	C. C. Babington, *Manual of British Botany*, 9th ed.
Boul.	N. Boulay in Rouy et Camus, *Flore de France*, tome VI.
Coste	N. Boulay in Coste, *Flore de la France*, tome II.
Fl. Dan.	Oeder and others, *Icones Florae Danicae*.
Focke Syn.	W. O. Focke, *Synopsis Ruborum Germaniae*.
Foerst.	Dr Foerster, *Flora excursoria Aachen*.
Hooker	J. D. Hooker, *The Students Flora of the British Islands*, 3rd ed.
Phyt.	*The Phytologist*.
Rog.	W. M. Rogers, *Handbook of British Rubi*.
Syme	*English Botany*, 3rd ed. by J. T. Boswell Syme.
Sud.	H. Sudre, *Rubi Europae*.

Key to sections of Eubatus

Lateral or basal lts. sess. or subsess. Stip. often broad, lin.-lanc. Pks. usu. pat. (Drupelets often large and in part defective. Fls. usu. from late May or early June till Sept. In some respects recalling *R. caesius*.) CORYLIFOLII

Stem not rooting, suberect or high-arching, glabrous or sli. pil. Pan. simple or hardly compound. Sep. green outside. (Rootstock often creeping or roots suckering. Ls. often 7-nate, falling in aut. Fls. in late May and June.) SUBERECTI

Stem rooting.

    I. Stem pks. *subequal*, seated *on or near the angles*.

        (*a*) Stkd. gls. acic. and pkts. *inconspicuous, rare or wanting*.

           1. *Eglandr.* Ls. *white* or gyish-white ben. becoming subcoriaceous. *Sep. refl.* Fls. showy. DISCOLORES

           2. Sli. glandr. *Stem slender*, procumbent or climbing. Ls. thin, green, gyish. or gyish.-white ben. *Fls. small* (<2 cm.), or larger and crumpled. *Sep. pat. or clasping. Stam. short.* SPRENGELIANI

           3. Sli. glandr. or eglandr. Ls. thin green gyish or gyish-white ben. Fls. usu. large. Sep. refl., pat., or erect. *Stam. usu. long.* SILVATICI

        (*b*) *Pkts. conspicuous*, rather fqt., *stkd. gls. and acic. few. Plant usu. a good deal hairy.* VESTITI

        (*c*) Stkd. gls. acic. (and usu. pkts.) *numerous.*

           1. Stkd. gls. acic. and pkts. *short and subequal* on the stem, sli. less so on petio. petiolules and pan. RADULAE

           2. Stkd. gls. acic. and pkts. *evidently unequal.*

               (α) Stkd. gls. acic. and pkts. *often few on the stem*, esp. on the lower part. Terminal lt. often roundish cuspidate, rather finely evenly toothed. ROTUNDIFOLII

               (β) Stkd. gls. acic. and pkts. *numerous, mod. unequal* but not passing into pks. Pan. usu. broad, equal, truncate. APICULATI

               (γ) Stkd. gls. acic. (and pkts. if present) *more unequal* but still not passing into pks. Pan. well developed, often pyramidal and ending in a raceme. Sep. attenuate, leafy-appendiculate. GRANDIFOLII

    II. Pks. *very unequal, scattered all round the stem*, usu. passing into acic. or stkd. gls.

        (*a*) Stem angled, low-arching then procumbent, with some pks. strong-based. Pan. well developed, middle branches cymose. Fls. usu. showy, often pink. HYSTRICES

        (*b*) Stem blunt-angled or terete, usu. prostrate. Pks. often weak and resembling acic. Pan. small, middle branches racemose, often divided to base. Pet. usu. white, narrow, rather small. GLANDULOSI

Key to subsections and series of Eubatus

Sect. SILVATICI

Ls. mostly green ben. Sep. erect, pat. or refl.   Subsect. *Virescentes* Genev.
  Strongly armed. Stem and ls. glabrescent.   *Calvescentes*
  Mod. armed. Stem, ls. and pan. pil.
    Ls. softly hairy or pubesc. ben. at first, afterwards ±glabresc. Rather weakly armed.   *Macrophylli*
    Ls. thick, abundantly, bifariously pil. on the veins ben. More strongly armed.   *Pyramidales*
  Weakly armed. Pks. subulate or acicular, small.   *Nemorenses*
Ls. markedly greyish-white ben. Strongly armed.   *Discolorides*
  Stem with crisp, pat. hair. Pks. strong and long, subul.-lanc., often sli. sigmoid or ascending. Ls. pubesc. and/or ±felted ben.   *Subvirescentes*
  Stem pil. or glabr. Pks. mod. long. Ls. more closely felted ben. Usu. sparsely glandr.   *Subdiscolores*
  Stem glabr., or nearly so. Pks. pat. or sli. ascending, slender. Eglandr.   *Imbricati*

Sect. DISCOLORES

    Stem arcuate-procumbent, usu. red or purp., perennial.
        Stem pruin. ±scaly and waxed on the side turned towards the sun. Stam. long or short.   *Gypsocaulones*
        Stem epruin. Pan. often subpyram. Stam. long. (Plant often robust.)   *Hedycarpi*
    Stem tall arcuate, usu. sulc., usu. green, often biennial.
        Stem epruin. Ls. silvery greyish white felted ben. (rarely greenish grey) and often somewhat silky or velvety.
                                                                Candicantes

Sect. VESTITI

    Ls. green ben. (upper ones sometimes gyish. ben.)   Series *Virescentes* Sud.
    Ls. grey or white, felted, and pubesc. or pil. ben.   *Hypoleuci*

Sect. RADULAE

    Ls. ±grey or white ben.   *Micantes*
    Ls. green ben. (upper ones sli. grey ben.)   *Concolores*

Sect. APICULATI

    Pet. white or pinkish (rarely pink). Stam. white. Sty. often red.
        Pan. and usu. stem pil.
            Sep. refl. or pat. (rarely some erect). Pedunc. sometimes fasciculate or deeply divided.   *Foliosi*
            Sep. uniformly clasping.   *Pallidi*
        Pan. and stem shortly pil. pubesc. or felted.
            Stem and flg. branch pks. short. Ls. 3 (5)-nate, evenly, min. to mod. serr.-dent. Sep. pat. to erect.
                                                                       Scabri
    Pet. (and often stam. and sty.) pink or rose.
        Pan. rachis often pil.-hirsute.   *Obscuri*
    Pet. rose, pink or pinkish (rarely white). Sty. greenish, yellowish or pinkish.
        Stem. armature in some spp. scanty. Pan. pks. in some spp. very long or very short, or very hooked.
        Pan. branches not fasciculate. Ls. not all, nor mostly, 3-nate, nor min. toothed.   *Incompositi*

Sect. GLANDULOSI

    Pks. strong, often curved, on a strong, broad base.   ¨ *Feroces*
    Pks. weak, on a ±conical base.   *Imbelles*

Sect. CORYLIFOLII

Characters of *R. caesius* mixed with those of sect. SILVATICI	*Sub-Silvatici*
,, ,, ,, ,, ,, ,, ,, ,, DISCOLORES	*Sub-Discolores*
,, ,, ,, ,, ,, ,, ,, ,, RADULAE	*Sub-Radulae*
,, ,, ,, ,, ,, ,, ,, ,, HYSTRICES or GLANDULOSI	*Sub-Glandulosi*

Notes. (i) The colour of the parts of the flower must be observed through a lens on the opening flower, as the colour quickly fades after expansion.

(ii) Descriptions of the posture of the sepals always relate to the temporary stage reached soon after the petals fall from the flower and the carpels begin to swell—not to the posture during flowering, nor on the coloured fruit.

Latin diagnoses of the new Section and Series in the List are appended, in compliance with the international rules.

Sectio nova *Rotundifolii*. Typus, *R. rotundifolius* (Bab.) Blox. in Kirby. Aculei sat aequales. Glandulae stipitatae, aciculi, aculeolique inaequales, nonnunquam ad inferum turionem rariores vel subnulli. Foliola plerumque subrotunda vel obovata, tenuiter serrata.

Sectio *Apiculati* Focke.

Series nova *Foliosi*. Typus, *R. foliosus* Weihe. Petala alba vel dilute rosea, raro rosea. Stamina alba. Styli saepius rubri. Panicula turioque hirsutae. Sepala reflexa vel patula, interdum in parte erecta. Pedunculi saepe fasciculati vel saltem alte divisi.

Series nova *Pallidi*. Typus, *R. pallidus* Weihe. Ut in *Foliosis*, sed sepala semper mox erecta.

Series nova *Scabri*. Typus, *R. scaber* Weihe. Flores ut in *Foliosis*, petala pro more alba. Panicula turioque pubescentes vel tomentosae. Aculei breves. Foliola regulariter minute vel mediocriter serrata dentata. Sepala patula vel erecta.

Series nova *Obscuri*. Typus, *R. obscurus* Kalt. Flores speciosi. Petala saepe cum staminibus stylisque rosea. Panicula vulgo piloso-hirsuta.

Series nova *Incompositi*. Typus, *R. apiculatus* Weihe. Flores vix sane speciosi, sed petala plerumque dilute rosea vel roseola, raro rosea. Turionis arma interdum pauca. Paniculae aculei aliquando longi ± patentes, aliquando breves, aliquando uncinati. Pedunculi haud fasciculati, nec foliola unquam ut in *Scabris*.

Sectio *Glandulosi* P. J. Muell.

Series nova *Feroces*. Typus, *R. Schleicheri* Weihe. Aculei validiores, basi lati compressi.

Series nova *Imbelles*. Typus, *R. hirtus* W. & K. Aculei debiles, basi vix compressi.

Sectio *Corylifolii* Focke.

Series nova *Sub-Radulae*. Typus, *R. adenoleucus* Chab. Aculei subaequales; glandulae stipitatae aciculique breves ± crebri, sicut in *Radulis*.

APPENDIX 2

LIST OF BRITISH SPECIES OF *HIERACIUM*, EXTRACTED FROM H. W. PUGSLEY'S MONOGRAPH NOW AWAITING PUBLICATION

Hieracium L.

Subgenus *EU-HIERACIUM*

Phyllopoda

Sect. *Amplexicaulia*

H. amplexicaule L.
H. pulmonarioides Vill.
H. speluncarum Arv.-Touv.

Sect. *Alpina*

H. alpinum L.
H. holosericeum Backh.
H. grovesii Pugsl.
H. eximium Backh.
H. calenduliflorum Backh.
H. macrocarpum Pugsl.
H. graniticolum W. R. Lint.
H. gracilentum Backh.
H. globosiflorum Pugsl. (globosum Backh., non Desf.)
H. pseudopetiolatum (Zahn) Roffey (petiolatum Hanb.)
H. backhousei Hanb.
H. pseudocurvatum (Zahn) Pugsl. (nigrescens Backh. non Willd.)
H. nigrescens Willd.
H. hanburyi Pugsl. (chrysanthum Backh., non Ledeb.)
H. subgracilentipes (Zahn) Roffey

Sect. *Subalpina*

H. lingulatum Backh.
H. molybdochroum Dahlst.
H. marshallii Lint.
H. cremnanthes (Hanb.) Pugsl.
H. sinuans Hanb.
H. senescens Backh.
H. pseudanglicum Pugsl.
H. gracilifolium (Hanb.) Pugsl.
H. submurorum Lindbg.
H. cumbriense Hanb.
H. centripetale Hanb.
H. hyparcticoides Pugsl.
H. isabellæ E. S. Marsh.
H. callistophyllum Hanb.
H. dasythrix (Lint.) Pugsl.

Sect. *Cerinthea*

H. anglicum Fr.
H. brigantum (Hanb.) Roffey
H. ebudicum Pugsl.
H. hebridense Pugsl.
H. ampliatum (W. R. Lint.) Ley
H. petrocharis (Lint.) W. R. Lint.
H. langwellense Hanb.
H. flocculosum Backh.
H. shoolbredii E. S. Marsh.
H. iricum Fr.
H. scarpicum Pugsl.

Sect. *Oreadea*

H. lima Hanb.
H. lasiophyllum Koch
H. eustomon (Lint.) Roffey
H. schmidtii Tausch
H. leyi Hanb.
H. nitidum Backh.
H. basicrinum (Zahn) Roffey
H. sommerfeltii Lindbg.
H. carneddorum Pugsl.
H. argenteum Fr.
H. vagense Ley
H. cambricum (Baker) Hanb.
H. griffithii Hanb.
H. deganwyense Pugsl.
H. buglossoides Arv.-Touv.
H. scoticum Hanb.
H. chloranthum Pugsl. (pseudonosmoides W. R. Lint.)
H. beebyanum Pugsl.
H. orimeles Hanb.

Sect. *Sub-Oreadea*

H. rubicundum Hanb.
H. caledonicum Hanb.
H. pseudorepandum Pugsl. (repandum Ley, non Schrank)
H. riddelsdellii Pugsl.
H. basalticolum Pugsl.
H. jovimontis (Zahn) Roffey
H. cyathis (Ley) W. R. Lint.
H. hypochaeroides Gibson
H. subplanifolium Pugsl.
H. britannicum Hanb.
H. dasypodum Dahlst.
H. britanniciforme Pugsl.
H. clovense Lint.
H. fratrum Pugsl. (sordidum W. R. Lint., non Gillies)

Sect. *Vulgata*

Subsect. *Bifida*

H. pachyphyllum (Purchas) Williams
H. sanguineum (Ley) W. R. Lint.
H. tricolorans (Zahn) Pugsl.
H. subcyaneum (W. R. Lint.) Pugsl.
H. silvaticoides Pugsl.
H. maculosum Dahlst.
H. pseudo-sarcophyllum Pugsl.
H. anguinum (W. R. Lint.) Roffey
H. neocoracinum Pugsl.
H. prolixum Norrlin
H. subtenue (W. R. Lint.) Roffey
H. aggregatum Backh.
H. oxyodus W. R. Lint. emend.

Subsect. *Stellatifolia*

H. cillense Pugsl.
H. cymbifolium Purchas

Subsect. *Glandulosa*

H. praecox Schultz-Bip.
H. duriceps Hanb.
H. killinense (Zahn) Roffey
H. praetenerum Almq.
H. pellucidum Laest.
H. stenstroemii Dahlst.
H. exotericum Jord.
H. cuneifrons (Ley) Pugsl.
H. pulcherrimum (Hanb.) Roffey
H. itunense Pugsl.
H. pollinarium Hanb.
H. pictorum Lint.
H. pollinarioides Pugsl.
H. caliginosum (Dahlst.) Roffey
H. subprasinifolium Pugsl.
H. pseudo-stenstroemii Pugsl.
H. longilobum Dahlst.
H. semi-crassiceps Pugsl.
H. ciliatiflorum Pugsl. (ciliatum Almq., non Willd.)
H. variicolor Dahlst.
H. dipteroides Dahlst.

Subsect. *Sagittata*

H. oïstophyllum Pugsl. (sagittatum Lindbg., non H. & L.)
H. pycnodon Dahlst.
H. subhirtum (Hanb.) Pugsl.
H. rivale Hanb.
H. uisticolum Pugsl.
H. breadalbanense Hanb.
H. crebridentiforme Pugsl.
H. auratiflorum Pugsl.
H. lintonii Ley
H. euprepes Hanb.
H. orcadense W. R. Lint.
H. clivicolum (Hanb.) Pugsl.

Subsect. *Caesia*

H. angustatum Lindbg.
H. rhomboides (Stenström) Johanss.
H. melanochloricephalum Pugsl.
H. stenophyes W. R. Lint.
H. vennicontium Pugsl.
H. anfractiforme E. S. Marsh.
H. caesiomurorum Lindbg.
H. dissimile Lindbg.
H. subramosum Lönnroth
H. orarium Lindbg.
H. cravoniense (Hanb.) Roffey
H. rubiginosum Hanb.
H. caesiopilosum Pugsl.
H. decolor Ley
H. fulvocaesium Pugsl.
H. erythraeum Lint.
H. farrense Hanb.
H. proximum Hanb.
H. angustisquamum (Pugsl.) Pugsl.
H. eustales Lint.
H. insulare Hanb.
H. leyianum (Zahn) Roffey
H. holophyllum W. R. Lint.

Subsect. *Eu-Vulgata*

H. vulgatum (Fr.) Almq. (triviale Norrlin)
H. acroleucum Stenström

H. neopinnatifidum Pugsl. ined. (pinnatifidum Lönnroth, non Willd.)
H. lepidulum Stenström
H. maculatum Sm.
H. roffeyanum Pugsl.
H. surrejanum Hanb.
H. megapodium Dahlst.
H. subamplifolium (Zahn) Roffey
H. subminutidens (Zahn) Pugsl. (adlerzii Hanb., non Almq.)
H. diaphanum Fr.
H. praesigne (Zahn) Roffey
H. diaphanoides Lindbg.
H. rectulum Ley
H. pulchrius (Ley) W. R. Lint.
H. submutabile (Zahn) Pugsl.
H. daedalolepioides (Zahn) Roffey
H. anglorum (Ley) Pugsl.
H. tunbridgense Pugsl. ined.
H. lachenalii Gmelin (sciaphilum auct.)
H. strumosum Ley
H. acuminatum Jord.

Transitoria

Sect. *Alpestria*

H. dovrense Fr.
H. pulchelliforme (W. R. Lint.) Pugsl. ined. (pulchellum Williams, non Lindbg.)
H. zetlandicum Beeby
H. pseudo-protractum Pugsl. ined.
H. hethlandiae (Hanb.) Pugsl. ined.
H. australius (Beeby) Pugsl. ined.
H. subtruncatum Beeby
H. breve Beeby
H. praethulense Pugsl. ined.
H. vinaceum (Beeby) Pugsl. ined.
H. northroense Pugsl. ined.
H. dewarii Syme
H. perthense Williams

Sect. *Prenanthoidea*

H. prenanthoides Vill.
H. denticulatum Sm. (borreri Syme)

Sect. *Tridentata*

H. cacuminum Ley
H. hibernicum Hanb.
H. longiramosum Pugsl. ined.
H. cambricogothicum Pugsl. ined.
H. boreophilum (Zahn) Roffey
H. calcaricolum (Hanb.) Roffey
H. fragilicaule Pugsl. ined.
H. calviceps Pugsl. ined.
H. gothicoides Pugsl. ined.
H. uiginskyense Pugsl. ined.
H. trinitatis Pugsl. ined.
H. backhouseanum (Zahn) Roffey
H. pseudacrifolium Pugsl. ined.
H. scullyi W. R. Lint.
H. ardaricum Pugsl. ined.
H. stewartii (Hanb.) Roffey
H. subintegrifolium Pugsl. ined.
H. stictophyllum Dahlst.
H. sparsifolium Lindbg.
H. oligodon (Lint.) Pugsl. ined.
H. linguans (Zahn) Roffey
H. substrigosum (Zahn) Roffey
H. donegalense Pugsl. ined.
H. grandescens Dahlst.
H. placerophylloides Pugsl. ined.
H. hartianum Pugsl. ined.

H. tridentatum Fr.
H. scabrisetum (Zahn) Roffey
H. cantianum Hanb.
H. nidense (Hanb.) Roffey
H. trichocaulon (Dahlst.) Roffey
H. eboracense Pugsl. ined.
H. rhayaderense Pugsl. ined.
H. lissolepium (Zahn) Roffey

Aphyllopoda

Sect. *Foliosa*

H. latobrigorum (Zahn) Roffey (auratum
 auct. angl.)
H. drummondii Pugsl. ined.
H. neocorymbosum Pugsl. ined.
H. subcrocatum (Lint.) Roffey
H. bartonii Pugsl. ined.
H. subpolyphyllum Pugsl. ined. (polyphyllum
 Dahlst., non Willd.)
H. reticulatum Lindbg.
H. strictiforme (Zahn) Roffey
H. opsianthum (Dahlst.) Roffey
H. listeræ Pugsl. ined.
H. pseudamplidentatum Pugsl. ined.
H. bakeranum Pugsl. ined.
H. tavense Ley
H. pycnotrichum (Dahlst.) Roffey
H. maritimum Hanb.
H. obesifolium Pugsl. ined.

Sect. *Umbellata*

H. umbellatum L.
H. ogweni Lint.
H. bichlorophyllum (Druce & Zahn) Pugsl.
 ined.

Sect. *Sabauda*

H. obliquum Jord. emend.
H. sedunense (Gremli) Roffey
H. argutifolium Pugsl. ined.
H. eminentiforme Pugsl. ined.
H. virgultorum Jord.
H. rigens Jord.
H. vagum Jord.
H. sublactucaceum (Zahn) Druce
H. calvatum (Hanb.) Pugsl. ined.
H. subquercetorum Pugsl. ined.
H. croceostylum Pugsl. ined.

Subgenus *PILOSELLA*

Acaulia

Sect. *Pilosellina*

H. peleterianum Mérat
H. pilosella L.

Cauligera

Sect. *Auriculina*

H. lactucella Wallr. (auricula auct., non L.)
H. helveolum (Dahlst.) Pugsl. ined.

Sect. *Pratensina*

H. flagellare Willd.
H. colliniforme (NP.) Roffey
H. aurantiacum L.
H. brunneocroceum Pugsl.

Sect. *Praealtina*

H. praealtum Vill.
H. arvorum (NP.) Pugsl. ined.
H. spraguei Pugsl. ined.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1944

Income

	£ s. d.	£ s. d.
Subscriptions received, including arrears, and *less* Payments in advance:		
Members taking *Journal of Ecology* only ...	270 0 0	
Members taking *Journal of Animal Ecology* only	175 11 5	
Members taking both Journals ...	148 5 0	
Associates	1 10 0	595 6 5
Interest on Investments	62 5 3	
Interest on Deposit Account ...	1 15 11	
Profit on Redemption 5% Conversion Loan Stock ...		64 1 2
Grant from Royal Society ...		1 10 0
Journal of Ecology. Sales *less* Cost ...		150 0 0
Index to *Journal of Ecology*, vols. 1–20, Sales ...	9 10 0	241 6 4
Less Expenses	1 8 7	6 1 5
		£1,060 5 4

Journal of Ecology, 1944:

	£ s. d.	£ s. d.
Sales: Current vol. 32 ...	550 7 4	
Back volumes and parts ...	199 19 0	
Reprints of Papers ...	38 18 6	
		£789 4 10

Journal of Animal Ecology, 1944:

	£ s. d.	£ s. d.
Sales: Current vol. 13 ...	223 9 2	
Back volumes and parts ...	79 10 3	
Reprints of papers ...	28 6 0	331 5 5
		258 12 2
		£589 17 7
Balance (see above, under Expenditure) ...		

Expenditure

	£ s. d.	£ s. d.
Working Expenses:		
Printing and Stationery ...	3 18 4	
Postages	13 16 1	
Travelling	10 5 5	
Meeting Expenses ...	16 9 10	
Audit Fee	3 3 0	
Nature Reserves Committee, Bank Charges	1 2 7	
Clerical assistance	12 0 0	60 15 3
Grant: to Freshwater Biological Association		10 0 0
Biological Flora of the British Isles:		
Cost of Printing	117 2 10	
Less Sales	20 18 2	96 4 8
Journal of Animal Ecology. Cost *less* Sales ...		258 12 2
Balance—Surplus for the Year (To Balance Sheet)...	425 12 1	
	634 13 3	
		£1,060 5 4

Journal of Ecology, 1944:

	£ s. d.	£ s. d.
Costs: Paper, Blocks, Printing and Binding	424 11 8	
Publishers' Commission ...	103 3 3	
Carriage, etc. ...	13 16 8	
Insurance of Stock ...	6 6 11	547 18 6
Balance (see above, under Income) ...		241 6 4
		£789 4 10

Journal of Animal Ecology, 1944:

	£ s. d.	£ s. d.
Costs: Paper, Blocks, Printing and Binding	512 5 7	
Publishers' Commission ...	47 11 5	
Carriage, etc. ...	10 6 6	
Insurance of Stock ...	9 14 1	
Fee for checking references	10 0 0	
		£589 17 7

BALANCE SHEET AT 31 DECEMBER 1944

Assets

	£ s. d.	£ s. d.
Cash at Bank: Current Account	150 17 2	
Deposit Account	350 0 0	
		500 17 2
Publishing Accounts—Amounts due from Cambridge University Press:		
Journal of Ecology. Balance of Account ...	479 4 2	
Journal of Animal Ecology. Balance of Account...	161 13 11	
Journal of Ecology. Index Volume ...	8 1 5	
Biological Flora of the British Isles ...	17 18 8	
		666 18 2
Investments at Cost:		
Held 31 December 1943—		
£1,200 of 3½% War Loan	1,230 4 1	
£300 of 3% Savings Bonds	300 0 0	
Purchased Jan./May 1944—		
£100 of 3% Savings Bonds	400 0 0	
		1,930 4 1
		£3,097 19 5

A further Asset, not valued, is the Unsold Stock of Journals and Index Volume held by the Publishers for the Society.

VICTOR S. SUMMERHAYES
ALEX. S. WATT
Hon. Treasurers.

Liabilities

	£ s. d.	£ s. d.
Members' Subscriptions, prepaid for 1945/7...		19 16 9
Library Fund		1 5 0
Printing Accounts due to the Cambridge University Press:		
Journal of Ecology, vol. 32, no. 2 and Reprints ...	163 16 5	
Journal of Animal Ecology, vol. 13, no. 2 and Reprints ...	235 6 3	
Biological Flora, from *Journal of Ecology,* vol. 32, no. 2 & Reprints ...	84 12 1	
		483 14 9
General Revenue Account:		
Balance in hand 31 December 1943	1,958 9 8	
Surplus for 1944	634 13 3	
		2,593 2 11
		£3,097 19 5

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1945

Income

	£ s. d.	£ s. d.
Subscriptions received, including arrears, and *less* Payments in advance:		
Members taking *Journal of Ecology* only ...	278 12 6	
Members taking *Journal of Animal Ecology* only ...	161 6 2	
Members taking both Journals ...	153 0 0	
Associates ...	15 0	
	593 13 8	
Less Reserve allocated to second part of each Journal, not yet published ...	230 0 0	
		363 13 8
Interest on Investments ...	64 13 0	
Interest on Deposit Account ...	2 16 7	
		67 9 7
Journal of Ecology. Sales *less* Cost ...		18 15 10
Journal of Animal Ecology. Sales *less* Cost ...		2 1 6
Index to *Journal of Ecology*, vols. 1–20:		
Sales ...	4 12 0	
Less Expenses ...	19 2	
		3 12 10
		£455 13 5

Journal of Ecology, 1945, Part 1:	£ s. d.
Sales: 50% Current vol. 33, part 1	234 1 3
Back volumes and parts ...	109 17 0
Reprints of papers...	7 7 2
	£351 5 5

Journal of Animal Ecology, 1945:	£ s. d.
Sales: 50% Current vol. 14, part 1	95 11 0
Back volumes and parts ...	148 8 0
Reprints of papers ...	15 15 0
	£259 11 0

Expenditure

	£ s. d.	£ s. d.
Working Expenses:		
Printing and Stationery ...	15 18 3	
Postages ...	8 2 2	
Travelling ...	8 7 7	
Will Life Conservation Memorandum ...	14 15 0	
Meeting Expenses ...	6 12 6	
Audit Fee ...	6 6 0	
Bank Charges and Typing ...	6 18 0	
Clerical assistance ...	13 0 0	
		73 19 6
Grant: to Freshwater Biological Association ...		10 0 0
Subscription: to Parliamentary and Scientific C'tee ...		10 10 0
Biological Flora of the British Isles:		
Costs of Printing, Commission, &c. ...	62 13 8	
Less Sales of Reprints ...	18 1 5	
		44 12 3
Balance—Surplus for the Year (To Balance Sheet) ...		139 1 9
		316 11 8
		£455 13 5

Journal of Ecology, 1945, Part 1:	£ s. d.	£ s. d.
Costs: Vol. 33, part 1:		
Paper, Blocks, Printing and Binding	267 0 0	
Publishers' Commission ...	49 4 6	
Carriage, etc. ...	8 8 1	
Insurance of Stock ...	8 0 0	
	332 9 7	
Balance (see above, under Income) ...	18 15 10	
	£351 5 5	

Journal of Animal Ecology, 1945:	£ s. d.	£ s. d.
Costs: Vol. 14, Part 1		
Paper, Blocks, Printing and Binding	199 9 2	
Publishers' Commission ...	34 16 5	
Carriage, etc. ...	5 6 11	
Insurance of Stock ...	8 0 0	
Fee for checking references ...	10 0 0	
	257 12 6	
Balance (see above, under Income) ...	2 1 6	
	£259 14 0	

BALANCE SHEET AT 31 DECEMBER 1945

Assets

	£ s. d.	£ s. d.
Cash at Bank: Current Account	606 18 1	
Deposit Account	100 0 0	
		706 18 1
Publishing Accounts—Amounts due from Cambridge University Press:		
Journal of Ecology. Balance of Account ...	276 19 2	
Journal of Animal Ecology. Balance of Account...	105 15 8	
Journal of Ecology. Index Volume	3 12 10	
Biological Flora of the British Isles	15 5 3	
		401 12 11
Investments at Cost:		
Held 31 December 1944—		
£1,200 of 3½% War Loan	1,230 4 1	
£700 of 3% Savings Bonds, 1960/70 ...	700 0 0	
Purchased 9 June 1945—		
£300 of 3% Savings Bonds, 1965/75 ...	300 0 0	
		2,230 4 1
		£3,338 15 1

Liabilities

	£ s. d.	£ s. d.
Members' Subscriptions, prepaid for 1946/7... ...		17 1 9
Library Fund		1 5 0
Printing Accounts due to the Cambridge University Press:		
Journal of Ecology, Balance of Account	33 19 9	
Sundry Printing and Stationery	36 4 0	
		70 3 9
Subscription due to Parliamentary and Scientific Committee		10 10 0
Grant towards paper in Journal of Animal Ecology ...		100 0 0
Reserve of Subscriptions for 1945 allocated to second part of each Journal...		230 0 0
General Revenue Account—Surplus in Hand:		
Balance at 31 December 1944	2,593 2 11	
Surplus for year 1945	316 11 8	
		2,909 14 7
		£3,338 15 1

A further Asset, not valued, is the Unsold Stock of Journals, Index Volume and Biological Flora Reprints held by the Publishers for the Society.

VICTOR S. SUMMERHAYES
ALEX. S. WATT
Hon. Treasurers.

Audited and found correct, and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

WM NORMAN & SONS
Chartered Accountants.

120 BISHOPSGATE, E.C. 2
and
231a HIGH ROAD, LOUGHTON, ESSEX.
6 *March* 1946.

LIST OF MEMBERS (16 JANUARY 1946)

E. = Takes *The Journal of Ecology*.   A. = Takes *The Journal of Animal Ecology*

Corrections, omissions or changes of address should be notified at once to the
Hon. Secretary, Dr H. GODWIN, Botany School, Cambridge

E.	**Abery**, Miss W.; Provincial Education Office, Kampala, Uganda.
E.	**Abeywickrama**, B. A., B.Sc.; Dept. of Botany, University of Ceylon, Colombo, Ceylon.
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E.	**Anand**, P. L., M.Sc.; Dept. of Biology, Sanatana Dharma College, Lahore, India.
E.	**Andersonian Naturalists' Society** (cf. Glasgow).
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E.	**Ashby**, Prof. Eric, D.Sc.; The University, Sydney, N.S.W.
	Ashby, K. R., B.A.; Wray Castle, Ambleside, Westmorland (*Associate Member*).
E.	**Bacon**, Mrs Alice; The Technical College, Brighton.
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E.	**Baxter**, Miss E. V., F.L.S.; The Grove, Upper Largo, Fife.
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E.	**Blackman**, Prof. G. E.; Univ. School of Rural Economy, Oxford.
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